Vol. IX 25.6.1957 No. 4

HYDROBIOLOGIA

ACTA HYDROBIOLOGICA, HYDROGRAPHICA ET PROTISTOLOGICA

UITGEVERIJ Dr W. JUNK — DEN HAAG — 1957

Données récentes sur la biologie des Poissons dans le delta central du Niger

par

J. Daget

(Institut Français d'Afrique Noire, Laboratoire d'Hydrobiologie, Diafarabé, Soudan français)

Les fleuves à régime tropical soudanien sont des fleuves à crue annuelle régulière; ils sont caractérisés par une grande différence de débit entre l'unique saison des pluies et la saison sèche. Lorsqu'ils traversent des régions sans relief, ils débordent leur lit majeur et inondent des surfaces plus ou moins vastes. Un exemple typique est fourni par le Moyen Niger qui, sur le territoire du Soudan français, possède une zone d'inondation atteignant en certains endroits plus de 100 kilomètres de large. L'existence d'une région aussi étendue et qui, chaque année, se trouve totalement recouverte par la crue du fleuve alors qu'à l'étiage il n'y subsiste d'eau que dans certains fonds de cuvette, pose des problèmes d'ordre hydrobiologique tout à fait particuliers et sans analogues dans les pays tempérés.

Nous n'examinerons ici que ceux concernant les Poissons dans le secteur deltaïque et qui sont depuis quelques années l'objet de recherches suivies, entreprises sous l'égide de l'Institut Français d'Afrique Noire. Le secteur deltaïque, appelé aussi delta central, est situé entre 13°30′ et 15°25′ de latitude N., et entre 3°45′ et 5°30′ de longitude W.; il est limité au nord par une ligne de faibles hauteurs, au pied desquelles s'étendent le lac Débo et le lac de Korienzé; à l'est par les collines gréseuses du plateau dogon; à l'ouest par la savane broussailleuse sahélienne. Le Niger y reçoit l'un de ses affluents les plus importants, le Bani. Au maximum de la crue, la surface recouverte par les eaux est d'environ 17.000 km², à peu de chose près compris dans les limites administratives des deux cercles de Macina et Mopti.
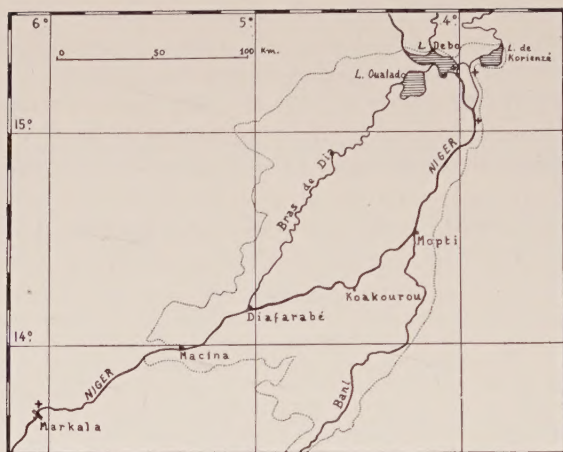
Fig. 1.

Le secteur deltaïque de la zone d'inondation du Moyen Niger. En pointillé, limite de la zone inondée; +, affleurements rocheux.

1. LE MILIEU

Dans le secteur deltaïque, pays amphibie par excellence, tous les phénomènes biologiques sont étroitement conditionnés par la crue du fleuve, aussi convient-il de commencer par préciser les modalités de celle-ci. Bien que les pluies locales puissent débuter en avril et durer jusqu'en novembre, plus de 90% des précipitations sont réparties sur les quatre mois de juin, juillet, août et septembre, qui constituent ce que l'on peut appeler la saison des pluies. Le secteur deltaïque reçoit en moyenne un peu plus de 500 mm, mais le fleuve n'y bénéficie pratiquement d'aucun apport de ruissellement, aussi la notion de bassin versant y est-elle sans grande signification. Les premières pluies sont absorbées par la terre déshydratée durant la saison sèche, ou bien, là où le sol est imperméable, forment des flaques ou de petites mares qui s'évaporent assez rapidement au soleil. Par la suite, les pluies entrent, dans le bilan hydraulique, en déduction des pertes de débit fort importantes dues à l'évaporation et à l'infiltration. Mais on droit admettre que, dans la région considérée ici, la crue est uniquement due aux précipitations reçues par les bassins versants des cours supérieurs du Niger, du Bani et de leurs affluents.

A cause des pertes en eau et du retard à l'écoulement consécutif à l'emmagasinement dans le lit majeur et dans la zone d'inondation, le débit maximum va constamment en diminuant vers l'aval. Par contre, une grande partie des eaux ainsi emmagasinées fait progressivement

322

retour au fleuve durant la décrue, de sorte que les branches descendantes des courbes limnimétriques sont décalées, la période de hautes eaux augmentant de durée vers l'aval. Pour préciser davantage, considérons la crue à Mopti durant l'année 1952 qui semble avoir été moyenne. Le débit a varié de 115 m³/s le I juin, à 2909 m³/s du 18 au 20 novembre, soit dans la proportion de 1 à 25. A ces mêmes dates, la cote d'étiage et la cote maxima étaient respectivement de 280,27 m. et 286,58 m., ce qui donne une amplitude de crue de 6,31
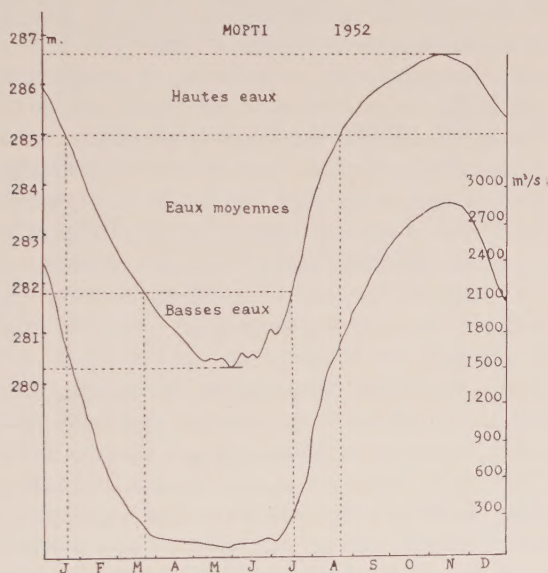
Fig. 2.

La crue à Mopti en 1952. En haut, cotes limnimétriques (chiffres à gauche); en bas, débits (chiffres à droite).

m. Si l'on appelle basses eaux les niveaux inférieurs à l'étiage augmenté du quart de l'amplitude, et hautes eaux les niveaux supérieurs à l'étiage augmenté des trois quarts de l'amplitude, la crue peut être schématisée de la façon suivante:

basses eaux	111 jours,	du 25 mars au 13 juillet
eaux moyennes de crue	41 jours,	du 14 juillet au 23 août
hautes eaux	150 jours,	du 24 août au 20 janvier
eaux moyennes de décrue	64 jours,	du 21 janvier au 24 mars

A Diafarabé, à l'entrée du secteur deltaïque et pour la même période, les basses eaux avaient duré 186 jours, les eaux moyennes de crue 40 jours, les hautes eaux 86 jours seulement et les eaux moyennes

de décrue 54 jours. Entre Diafarabé et Mopti, points situés par le fleuve à environ 120 kilomètres l'un de l'autre, les hautes eaux et les basses eaux ont donc des durées notablement différentes. A la sortie de la zone deltaïque, les différences par rapport à Mopti sont inverses de celles que l'on observe à Diafarabé, c'est à dire qu'au lac Débo les hautes eaux sont un peu plus longues et les basses eaux un peu plus courtes. En outre, les rives du fleuve étant surélevées par rapport à la zone inondable, et les eaux cheminant dans celle-ci par un lacis de bras et de „marigots'', la crue et la décrue sont d'autant plus tardives qu'il s'agit d'un point en communication moins directe avec le lit mineur. Mais les variations de niveau à l'intérieur de la zone d'inondation sont des fonctions trop complexes, et localement trop variables, de la crue du fleuve pour pouvoir être analysées de façon précise.

En aucun point du secteur deltaïque il n'existe d'eaux profondes. Dans le lit mineur du fleuve, il est rare de trouver à l'étiage des mouilles de plus de 5 mètres et les plus bas-fonds ne dépasseraient pas 10 mètres. Le lac Débo et ses annexes, le lac Ouallado et le lac de Korienzé, sont en réalité intermédiaires entre lacs et étangs; des premiers ils possèdent le nom et l'étendue d'eau libre de toute végétation, des seconds le fond plat et la faible profondeur. Dans ces conditions, courant et vents assurent un brassage de l'eau suffisant pour que l'on n'ait pas à tenir compte des phénomènes de stratification thermique. Naturellement, la température de l'eau présente des variations nycthémérales et des variations saisonnières qui suivent celles de la température de l'air, mais avec une amplitude très atténuée du fait de la grande capacité calorifique du milieu aqueux. A Diafarabé, en 1952, la moyenne des maxima, pris en surface et en eau courante, a varié de 30°5 en mai—juin à 22°1 en janvier; la moyenne des minima de 29°2 en juin—juillet à 20°6 en janvier. On retrouve sur la courbe de variation des moyennes mensuelles les deux maxima et les deux minima caractéristiques des climats soudanien et sahélien; mais de mai à octobre inclus, la température moyenne reste supérieure à 28°; nous verrons que cette période de l'année est celle où a lieu la reproduction et la croissance des poissons, à quelques exceptions près. Par contre, en décembre, janvier et février, la température moyenne reste inférieure à 22°5; il existe donc une période froide bien marquée et susceptible d'affecter la physiologie des poissons.

En eau stagnante et en l'absence de toute agitation, les couches superficielles se réchauffent et se refroidissent aux diverses heures de la journée, beaucoup plus rapidement que les couches profondes; l'absence de végétation ou au contraire la présence d'hélophytes qui protègent la surface à la fois de l'insolation, des courants d'air et de l'évaporation, influent également sur la température; mais celle-ci reste en moyenne voisine de celle des eaux courantes du fleuve. Ce-

pendant, en eau stagnante très peu profonde et sans végétation, en particulier sur la bordure des bancs de sable, on peut observer des températures extrêmes assez différentes. C'est ainsi que dans un endroit où se trouvaient des alevins de *Tilapia zilli*, nous avons noté 37° en mai à 14 h., et dans un autre où séjournaient des alevins de *Barilius niloticus*, 16°1 en fin décembre à 7 h. 30. A Diafarabé même, nous avons conservé des *Barbus* de diverses espèces dans un aquarium de plein air où la température est descendue certains matins de janvier à 10°, mais nous ne pensons pas que, dans les conditions naturelles, les poissons aient à supporter des températures aussi rigoureuses à l'intérieur du secteur deltaïque.
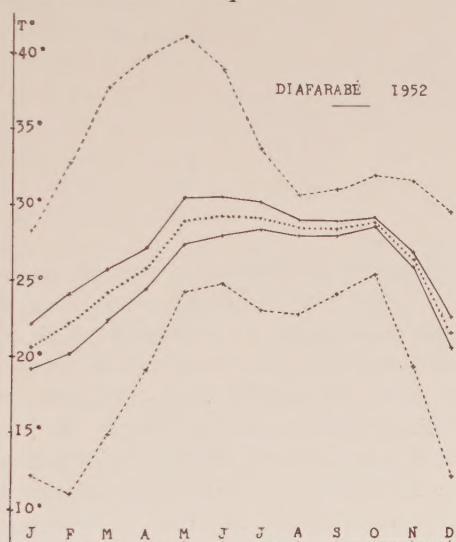
Fig. 3.

Températures à Diafarabé en 1952, moyennes mensuelles. En trait interrompu, températures maxima et minima de l'air. En trait plein, températures maxima et minima de l'eau courante. En pointillé, température moyenne de l'eau courante.

La transparence de l'eau n'est jamais grande dans le fleuve. Mesurée au disque de Secchi, elle n'exède pas 1 mètre aux basses eaux ni 0,50 m en période de crue. Cette turbidité est due beaucoup plus à la présence d'argile colloïdale que de sédiments ou de limons. Dans les mares d'eau de pluie et, en saison sèche, dans les mares de rétention dépourvues de végétation, la transparence est très faible: de 10 à 15 cm et dans certaines mares pas plus de 3 cm. Par contre, sur ces mêmes emplacements aux hautes eaux et lorsque la végétation est bien développée, le disque de Secchi peut être encore visible à plus de 2 mètres.

Au point de vue chimique, les eaux du fleuve, très peu minéralisées, sont sodi-calciques carbonatées et douées d'un faible pouvoir tampon. Il est intéressant de comparer les analyses de deux échantillons prélevés à Diafarabé le 14 juillet 1954, l'un dans le Niger et l'autre dans un puits creusé à quelques dizaines de mètres de la rive et alimenté par l'eau du fleuve. Les résultats sont les suivants:

		fleuve	puits
pH	sur le terrain	7,2	6,2
degré hydrotimétrique	,,	0°5	2°5 à 3°
alcalinité $N \times 10^{4-}$	,,	4	7
id.	au laboratoire	5	12
conductibilité électrique à 18°	,,	31	101,4
Na^+ mg. par litre		3	8
Ca^+ ,,		4	13,25
K^+ ,,		1,9	2,8
Mg^+ ,,		0	1,35
Cl^- ,,		1	3,75
SO^{4-} ,,		0	0

Les sulfates manquent totalement ou sont en quantité trop faible pour pouvoir être dosés, non seulement dans l'eau du fleuve, mais aussi dans la nappe phréatique. Les réserves en alcalins et alcalino-terreux sont minimes et l'on doit s'attendre à ce que la pauvreté en ces éléments ait une action limitative sur la productivité piscicole des eaux. Si le ruissellement sur la bassin versant du Haut Niger et de ses affluents dissout une certaine quantité de sels minéraux, ceux-ci se trouvent tellement dilués que leurs taux relatifs ne font que diminuer dans le secteur deltaïque au fur et à mesure de la montée de la crue. Le degré hydrotimétrique qui était, dans le fleuve, partout égal à 1 durant toute la période des basses eaux, devient pratiquement nul vers la fin août et ne remonte légérement que vers la fin septembre. L'alcalinité varie exactement de la même façon: de 7 $N \times 10^{-4}$ aux basses eaux, elle descend à 3,5 $N \times 10^{-4}$. On peut observer localement des phénomènes de ,,crue saline'', qui sont dus au lessivage de terrains restés longtemps asséchés et à la surface desquels se sont accumulés des déchets de toute sorte ou dans lesquels des remontées capillaires ont élevé la teneur superficielle en sels minéraux. C'est ainsi qu'à Diafarabé, le 16 juin 1954, dans l'eau qui traversait, pour la première fois de la saison, un vaste banc de sable, on put noter une montée brusque du degré hydrotimétrique de 1 à 2,5; mais le phénomène ne dura même pas vingt-quatre heures.

Les eaux non courantes sont en règle générale un peu plus riches que le fleuve aux mêmes dates. Dans la plaine inondée, aux hautes eaux, le degré hydrotimétrique varie de 1 à 2 et l'alcalinité de 3,5 à

4,75 N × 10⁻⁴. Dans les mares en saison sèche, les valeurs observées peuvent être plus élevées, ce qui est normal étant donné que ces milieux sont le siège d'une évaporation intense, entraînant une concentration progressive des substances dissoutes. Cependant, le degré hydrotimétrique ne dépasse pas 5, ni l'alcalinité 11,5 N × 10⁻⁴.

Dans le secteur deltaïque, les mesures de pH donnent des chiffres très variables et d'interprétation délicate. Les eaux du fleuve sont légèrement acides, ayant un pH compris entre 6 et 7, sauf durant la montée des eaux où le pH est voisin de 7,2. Localement et sous des influences diverses, on observe des valeurs différentes; c'est ainsi que près des rives où le courant n'assure pas un brassage efficace, la présence de débris végétaux abaisse le pH de 6,7 à 6,2; une pluie abondante le fait descendre de 7,2 à 6,4 et par contre, une „crue saline" le fait passer de 7,1 à 7,6. En eau stagnante, les variations sont encore plus accusées. Dans certaines mares le pH peut monter à 8. Expérimentalement, on a constaté que la seule présence de *Ceratophyllum demersum* faisait varier le pH de 7 à 7,8, suivant les heures de la journée et qu'une addition de bouse de vache le fait monter rapidement de 6,1 à 8,2. Dans des eaux aussi mal tamponnées, une mesure isolée de pH n'a pas grande signification; seules l'amplitude et le sens des variations pendant une assez longue période pourraient servir à caractériser un biotope donné.

2. LES POISSONS

La faune des Poissons du secteur deltaïque nous est maintenant bien connue; 112 espèces différentes y ont été capturées, dont nous donnons ci-dessous la liste.
(TC, très commune; C, commune; AC, assez commune; AR, assez rare; R, rare; TR, très rare; +, espèce ou sous-espèce existant dans la basse Gambie ou le Nil en territoire soudanais; △, espèce représentée par une autre sous-espèce dans la Basse Gambie ou le Nil).

		Gambie	Nil
Protopterus annectens (OWEN)	C	+	
Polypterus senegalus senegalus (CUVIER)	TC	+	△?
,, bichir lapradei (STEINDACHNER)	TC	+	△
,, endlicheri endlicheri (HECKEL)	C		+
Heterotis niloticus (CUVIER)	C	+	+
Notopterus afer GÜNTHER	TR	+	
Cromeria nilotica occidentalis DAGET	R		△
Microthrissa miri DAGET	AC		
Hyperopisus bebe occidentalis (GÜNTHER)	C	+	△
Mormyrus rume CUVIER et VALENCIENNES	C	+	

		Gambie	Nil
Mormyrus hasselquisti CUVIER et VALENCIENNES	AC	+	+
,, macrophthalmus GÜNTHER	AR		
Mormyrops deliciosus (LEACH)	AR	+	
Gnathonemus senegalensis elongatus (PFAFF)	TC	△	
,, niger (GÜNTHER)	C	+	+
,, deboensis DAGET	TR		
Petrocephalus bane ansorgei (BOULENGER)	C		△
,, bovei (CUVIER et VALENCIENNES)	TC	△?	+
Marcusenius psittacus BOULENGER	AR		
,, harringtoni BOULENGER	AR		+
,, isidori (CUVIER et VALENCIENNES)	TC	+?	+
,, lhuysi (STEINDACHNER)	AR		
Gymnarchus niloticus (CUVIER)	C	+	+
Hepsetus odoe (BLOCH)	C	+	
Hydrocyon brevis GÜNTHER	TC	+	+
,, somonorum DAGET	AR		
,, forskali CUVIER	TC	+	+
,, lineatus BLEEKER	AR		+
Alestes dentex sethente (CUVIER et VALENCIENNES)	TC	+	△
,, baremoze (JOANNIS)	TC	+	+
,, macrolepidotus (CUVIER et VALENCIENNES)	C		+
,, nurse RÜPPELL	TC	+	+
,, leuciscus GÜNTHER	TC	+	
Micralestes acutidens (PETERS)	TC		+
Nannaethiops unitaeniatus GÜNTHER	R	+	+
Distichodus brevipinnis GÜNTHER	TC	+	+
,, rostratus GÜNTHER	C	+	+
,, engycephalus GÜNTHER	AR		+
Paradistichodus dimidiatus (PELLEGRIN)	R	+	
Nannocharax ansorgei BOULENGER	R	+	
Citharinus citharus (GEOFFROY SAINT-HILAIRE)	TC	+	+
,, latus MÜLLER et TROSCHEL	TC		+
,, distichodoides PELLEGRIN	AC		
Citharidium ansorgei BOULENGER	AC		
Labeo senegalensis CUVIER et VALENCIENNES	TC	+	
,, coubie RÜPPELL	C	+	+
Barbus occidentalis BOULENGER	C		
,, deserti PELLEGRIN	C	+	
,, lepidus PFAFF	TC		
,, werneri BOULENGER	TC		+
,, macinensis DAGET	TC		
,, gourmansis PELLEGRIN	AC		
,, leonensis BOULENGER	C	+	+
,, stigmatopygus BOULENGER	AC		+
Barilius niloticus (JOANNIS)	TC		+
,, senegalensis STEINDACHNER	C	+	
Chelaethiops elongatus brevianalis DAGET	TC		
Clarias anguillaris (LINNÉ)	TC		+
Heterobranchus bidorsalis GEOFFROY SAINT-HILAIRE	C		+
,, longifilis CUVIER et VALENCIENNES	R	+	+

		Gambie	Nil
Schilbe mystus (LINNÉ)	TC	+	+
Eutropius niloticus (RÜPPELL)	TC		+
Siluranodon auritus GEOFFROY SAINT-HILAIRE	C		+
Physailia pellucida BOULENGER	TR		+
Arius gigas BOULENGER	AR		
Bagrus bayad macropterus PFAFF	TC		△
,, docmac niger DAGET	AC		△
,, filamentosus PELLEGRIN	AR		
Chrysichthys auratus longifilis (PFAFF)	TC		△
,, nigrodigitatus (LACÈPÈDE)	TC	+	
,, furcatus GÜNTHER	R	+	
Clarotes laticeps (RÜPPELL)	TC		+
,, macrocephalus DAGET	AC		
Auchenoglanis biscutatus (GEOFFROY SAINT-HILAIRE)	C		+
,, occidentalis (CUVIER et VALENCIENNES)	TC	+	+
Synodontis batensoda RÜPPELL	TC	+	+
,, membranaceus (GEOFFROY SAINT-HILAIRE)	TC	+	+
,, budgetti BOULENGER	C		
,, resupinatus BOULENGER	AR		
,, clarias (LINNÉ)	TC	+	+
,, sorex GÜNTHER	AC		+
,, eupterus BOULENGER	AC		+
,, filamentosus BOULENGER	AR		+
,, violaceus PELLEGRIN	AR		
,, nigrita CUVIER et VALENCIENNES	C	+	+
,, vermiculatus DAGET	R		
Synodontis ocellifer BOULENGER	AR	+	
,, schall (BLOCH SCHNEIDER)	TC		+
,, courteti PELLEGRIN	R		
,, gobroni DAGET	R		
Mochocus niloticus JOANNIS	AR		+
Malopterurus electricus (GMELIN)	C	+	+
Aphyosemion walkeri (BOULENGER)	AC		
Epiplatys senegalensis (STEINDACHNER)	TC	+	
,, bifasciatus taeniatus (PFAFF)	C	+	△
Aplocheilichthys gambiensis SVENSSON	TC	+	
,, pfaffi DAGET	TC		
Hemichromis fasciatus PETERS	TC	+	+
,, bimaculatus GILL	C	+	+
Tylochromis jentinki sudanensis DAGET	AC	△	
Pelmatochromis guentheri (SAUVAGE)	TR		
Tilapia galilaea (ARTÉDI)	TC	+	+
,, nilotica (LINNÉ)	TC		+
,, monodi DAGET	C		
,, zilli (GERVAIS)	TC		+
,, melanopleura DUMÉRIL	AR	+	
Gobiocichla wonderi KANAZAWA	TR		
Lates niloticus (LINNÉ)	TC		+

		Gambie	Nil
Ctenopoma petherici GÜNTHER[1])	C		+
Eleotris nana chevalieri (PELLEGRIN)	R		△
Parophiocephalus obscurus (GÜNTHER)	AC	+	+
Tetrodon fahaka strigosus (BENNETT)	C		△

Nous n'avons pas fait figurer dans la liste ci-dessus sept espèces qui ont été capturées à Markala, localité située un peu en amont du secteur deltaïque proprement dit. Ce sont les suivantes:

> Marcusenius petricolus DAGET
> Petrocephalus simus SAUVAGE
> Gnathonemus tamandua (GÜNTHER)
> Nannocharax fasciatus GÜNTHER
>   ,,   niloticus gracilis DAGET
> Garra waterloti (PELLEGRIN)

Ces espèces paraissent normalement cantonnées sur les fonds rocheux ou dans les rapides; elles sont plus ou moins communes dans le Haut Niger, et il est à prévoir que des individus isolés seront signalés un jour ou l'autre à l'intérieur du secteur deltaïque tel qu'il a été délimité plus haut. Le cas de *Gobiocichla wonderi* est particulièrement suggestif à cet égard. Il s'agit d'un petit Cichlidé pétricole hautement spécialisé et qui est relativement commun dans les trous de rochers de Markala. Or un individu a été capturé à Diafarabé même, c'est à dire à 145 kilomètres en aval de son biotope d'origine, hors duquel il avait vraisemblablement été entrainé. Un certain nombre d'espèces signalées comme rares ou très rares dans la liste ci-dessus appartiennent probablement au groupe de celles qui ont besoin de fonds rocheux, sinon pour subsister, du moins pour se reproduire. En effet, dans le delta central du Niger, il existe une grande variété de biotopes à eau courante ou stagnante, avec ou sans végétation et à fonds sableux, argileux ou vaseux, mais les cailloux et les rochers y sont extrêmement rares. Des affleurements de grès sont connus dans le lit mineur du fleuve un peu en amont de Mbouna, juste à l'entrée du lac Débo et en bordure de la zone inondée vers Sendégué. Ces biotopes rocheux, tous situés à l'extrémité nord-est du secteur deltaïque, sont en fait d'étendue très restreinte; ils ne constituent pas des seuils et ne donnent pas lieu à la formation de rapides.

Dans son ensemble, la faune ichthyologique du delta central nigérien doit être considérée comme riche et variée. On peut la com-

---

[1]) Et non *C. kingsleyae*, comme nous le montrerons dans une révision des *Ctenopoma* d'Afrique occidentale, en préparation.

parer à celle de la Basse Gambie, qui a été bien étudiée par SVENSSON (1933) et JOHNELS (1954), et à celle du bassin du Nil en territoire soudanais, qui a fait l'objet d'une récente mise au point par SANDON (1950). Or en Basse Gambie, 81 espèces seulement ont été signalées dont 19 appartiennent à la faune d'eau saumâtre ou sont des formes marines qui remontent en estuaire. Dans le Nil soudanais, 108 espèces ont été dénombrées, dont une, l'anguille commune, provient de la Méditerranée. Sur les 112 espèces du delta central du Niger, 33 se retrouvent à la fois dans la Basse Gambie et le Nil, 19 dans la Basse Gambie seulement et 33 dans le Nil seulement. Entre Nil et Niger il existe donc plus que des affinités faunistiques puisque 66 espèces, soit environ $60^{\circ}/_{\circ\circ}$, sont communes. Toutefois, la mise en place de ce stock commun doit être très ancienne car on constate souvent, entre les populations nigériennes (et probablement celles de toute l'Afrique occidentale) d'une part et les populations nilotiques d'autre part, des différences morphologiques minimes mais significatives. Nous citerons seulement l'exemple des *Alestes dentex*. Dans le delta central du Niger, le nombre de rayons bifurqués à la nageoire anale varie de 18 à 22; la moyenne calculée sur 428 individus est de 19,96, l'écart-type de 0,844, la distribution étant assimilable à une distribution normale. Pour le Nil par contre, BOULENGER donne des nombres variant de 19 à 23 et pour 50 individus, la moyenne est de 20,98, l'écart-type de 0,946. La différence entre ces deux moyennes est hautement significative: elle est supérieure à 7 fois l'écart-type correspondant. Elle ne peut donc pas être due aux hasards de l'échantillonnage. On doit conclure à l'existence de deux sous-espèces, *Alestes dentex dentex* (LINNÉ 1757) et *Alestes dentex sethente* (*C*. et *V*. 1849) la première différant de la seconde par un rayon de plus à l'anale. Il est à prévoir que des études biométriques plus précises et plus étendues que celles auxquelles on a procédé jusqu'à présent viendront allonger la liste des sous-espèces que nous avons fait figurer dans le tableau comparatif donné plus haut; ce tableau traduit seulement l'état actuel de nos connaissances et aura probablement à subir des retouches de détail lorsque la Systématique des Poissons d'eau douce africains aura fait de nouveaux progrès.

3. PÉRIODE DE REPRODUCTION

Dans le secteur deltaïque, la fraye de la plupart des Poissons a lieu durant une période de l'année bien déterminée et hors de laquelle on ne rencontre aucun individu sexuellement mûr. Cette période de reproduction coïncide à peu près avec la montée des eaux, mais elle peut durer plus ou moins longtemps suivant les espèces.

Chez les *Alestes*, tous les géniteurs, au début de la crue, possèdent des gonades au même degré de maturité. De jeunes alevins d'*Alestes dentex sethente*, mesurant 8 mm de longueur standard ont été récoltés le 5 août; d'autre part, à la décrue, les échantillonnages portant sur des jeunes sont homogènes et les longueurs observées sont distribuées normalement autour de la moyenne. Ceci montre que toutes les pontes sont bien groupées; elles doivent avoir lieu en fin juillet-début août. Chez *Heterotis niloticus*, la période de fraye est plus étalée. Des alevins de 28—39 mm de longueur standard ont été capturés dès le 8 août et des femelles d'ayant pas encore pondu le 18 septembre. Les pontes s'échelonnent donc sur trois mois, de juillet à septembre, mais le maximum de fréquence est en août. Comme les *Heterotis niloticus* déposent leurs oeufs dans des nids construits au milieu des herbes et en eau toujours peu profonde, les frayères ne sont fréquentées que durant quelques semaines, celles du mois de juillet sont localisées dans des zones basses tôt inondées, celles du mois de septembre dans des zones hautes inondées beaucoup plus tardivement. Les *Gymnarchus niloticus*, bien que déposant leurs oeufs dans des nids flottants, se reproduisent dans des conditions assez comparables à celles des *Heterotis*.

Certaines espèces qui frayent normalement aux hautes eaux dans les zones inondées, peuvent aussi effectuer des pontes précoces dans le lit mineur du fleuve. Tel est le cas de *Clarias anguillaris* dont les géniteurs pénétrent en août et septembre dans la plaine pour s'y reproduire, mais dont on a capturé des alevins mesurant de 18 à 34 mm de longueur standard le 24 juin, en bordure d'un banc de sable dans le Niger. C'est également le cas des *Tilapia* dont chaque femelle effectue plusieurs pontes successives à quelques semaines d'intervalle. *Tilapia zilli* par exemple commence à se reproduire dans le lit mineur du fleuve en avril et même en fin mars lorsque des conditions favorables se trouvent réalisées; mais les pontes s'échelonnent sur cinq ou six mois et le pourcentage des femelles ayant des ovules mûrs augmente régulièrement jusqu'en juillet. Les frayères de basses eaux, situées en bordure des bancs de sable, sont doublées par des frayères de hautes eaux situées dans la plaine d'inondation. Les échantillonnages effectués à la décrue sur les jeunes sont rarement homogènes; en les cumulant, on obtient pour les longueurs des courbes de fréquence irrégulières et l'écart entre les tailles minima et maxima est considérable.

Pour toutes les espèces qui se reproduisent à la montée des eaux et sur lesquelles nous possédons des renseignements suffisants, les pontes, qu'elles aient lieu dans le lit mineur, le lit majeur ou la plaine inondée, sont toujours terminées au moment où la crue est étale. Les espèces qui obéissent à un rythme différent et qui se reproduisent

durant la baisse des eaux, restent, jusqu'à plus ample informé, ex-
ceptionnelles. Nous ne pouvons en citer que deux en toute certitude:
Microthrissa miri, dont des alevins mesurant 8 à 15 mm de longueur
standard ont été récoltés le 11 décembre à Diafarabé, et *Barilius
niloticus* dont des alevins mesurant de 9 à 10 mm ont été récoltés le
2 janvier également à Diafarabé.

Il est certain que la reproduction des Poissons est sous le contrôle
de glandes endocrines, notamment de l'hypophyse, et que la tempé-
rature de l'eau joue un rôle de stimulant. Toutefois, si une certaine
température est nécessaire pour que les gonades arrivent à mûrir leurs
produits, d'autres facteurs, peut-être d'ordre trophique, exercent une
action non moins importante. Le fait est bien mis en évidence dans le
cas des *Tilapia zilli;* les individus qui se trouvent dans le lit mineur
du fleuve commencent à se reproduire en avril, alors que ceux qui se
trouvent dans des mares n'ont pas encore commencé en juin, ainsi
qu'il apparait dans le tableau suivant:

Mois	% de femelles ayant des ovules mûrs	
	fleuve	mares
Novembre—Mars	0 %	0 %
Avril	31	0
Mai	57	0
Juin	—	0
Juillet	97	—

Les poissons du secteur deltaïque, à part quelques rares exceptions
comme *Microthrissa miri* et *Barilius niloticus* signalées plus haut,
présentent une adaptation de fait à la reproduction en eaux chaudes,
puisque durant la période des pontes la température moyenne ne
descend pas au dessous de 28°. Il en résulte que les durées d'incu-
bation sont remarquablement courtes et le développement des ale-
vins rapide. Nous signalerons pour terminer que les espèces qui dé-
posent leurs oeufs dans des eaux peu profondes et non courantes les
placent dans des conditions telles que les embryons subissent des
variations de température importantes au cours de leur organogenèse.
Suivant les heures de la journée, on a noté en mai, dans un nid de
Tilapia zilli des températures variant de 26°2 à 31° et en août, dans un
nid d'*Heterotis niloticus*, des températures variant de 28° à 33°2, soit
des écarts de l'ordre de 5° entre le matin et l'après-midi.

4. MIGRATIONS

Beaucoup de poissons du secteur deltaïque effectuent des déplacements saisonniers: ce sont des migrateurs holobiotiques potamiques, aucun n'allant jusqu'à la mer qui est d'ailleurs à plus de 2500 km. D'un point de vue purement descriptif, on peut distinguer des migrations longitudinales, dans le lit mineur du fleuve, soit en remontant le courant, migrations anadromes, soit en le descendant, migrations catadromes, et des migrations latérales, du lit mineur vers le lit majeur ou la plaine d'inondation à la crue et en sens inverse à la décrue. Le même poisson peut effectuer successivement une migration longitudinale et une migration latérale, comme nous en verrons des exemples plus loin.

Les migrations anadromes sont les mieux connues; elles se poursuivent en effet en amont du secteur deltaïque, jusqu'au barrage de Markala, lequel est muni d'une passe à poissons, fonctionnant à la montée et à la baisse des eaux, où les observations sont particulièrement faciles. *Gnathonemus senegalensis elongatus*, par exemple, remonte dans la passe au mois d'août; il s'agit d'adultes sexuellement mûrs. A la même époque, vers Diafarabé, cette espèce qui ne se trouvait pas dans le lit mineur du fleuve aux basses eaux, y fait son apparition venant de l'aval. Les *Gnathonemus* remontent le courant jusqu'à ce qu'ils aient trouvé un endroit propice pour rentrer dans le lit majeur ou la plaine; ils suivent ensuite le sens d'écoulement de l'eau pour arriver jusque sur les lieux de ponte. La migration anadrome est donc suivie d'une migration latérale.

Cependant, toutes les migrations anadromes que l'on peut observer à la montée des eaux, ne sont pas le fait de géniteurs en quête de frayères. Toujours au mois d'août, on voit dans la passe à poissons de Markala des individus immatures remonter en même temps que des adultes sexuellement mûrs, et aussi des *Barilius niloticus* qui ne sont pas, eux, en période de reproduction. D'ailleurs les migrations anadromes de décrue, beaucoup plus importantes que celles de crue par le nombre de poissons qui y participent, n'ont certainement rien à voir avec la fraye. Les plus connues sont celles d'*Alestes leuciscus;* elles s'effectuent par bancs successifs dont la formation et la marche dépendent étroitement de la lunaison. On remarquera à ce propos que le fait n'a rien d'extraordinaire; un certain nombre de poissons tropicaux, appartenant à des groupes variés, ne manifestent d'activité migratrice qu'à des périodes bien déterminées du cycle lunaire. Ce phénomène a été récemment mis en évidence au Cambodge par BLACHE et GOOSSENS (1954), qui ont montré en outre que des troubles atmosphériques (chutes de pression barométriques et orages) semblaient perturber la marche des migrateurs. En tous cas, les façons de réagir

aux influences sidérales et météorologiques sont purement spéci-fiques. C'est ainsi que les *Alestes nurse* ne manifestent aucunement la même sensibilité au rythme lunaire que les *Alestes leuciscus*, de sorte que ces deux espèces voisines ne se trouvent qu'accidentellement mé-langées au cours de leurs migrations.

De nombreux carnassiers suivent les bancs d'*Alestes leuciscus* au dépens desquels ils se nourissent pendant une bonne partie de l'an-née; par conséquent, ils effectuent la même migration anadrome que leurs proies. Parmi les autres poissons qui remontent le courant à la décrue, citons encore *Labeo senegalensis* qui se déplace en bancs. WELMAN (1948) a signalé qu'en Nigéria *Barbus occidentalis* effectue au moment de la montée des eaux une migration anadrome de repro-duction. Dans le secteur deltaïque, il semble au contraire que cette espèce remonte le courant à la décrue, c'est à dire pendant la période de repos sexuel; on en voit franchissant la passe à poissons de Markala en décembre.

Certaines de ces migrations anadromes impliquent de longs par-cours. Nous avons suivi la marche d'un banc d'*Alestes leuciscus* depuis Kouakourou jusqu'à la limite amont de la zone d'inondation, soit sur environ 125 km; il n'est pas douteux qu'une partie au moins des poissons venant de Kouakourou ait remonté jusqu'à Markala, soit environ 215 km. Il est probable que la plupart des migrateurs ne parcourent que des distances plus faibles, mais il en est qui doivent aller du lac Débo à Markala, ce qui représente 400 km. Quant aux migrations catadromes, nous ne pouvons encore faire état d'aucune observation constituant une preuve formelle de leur existence; il serait cependant difficile de ne pas en admettre la réalité, ne fut-ce qu'en contre-partie des migrations anadromes.

Toutes les migrations longitudinales sont arrêtées durant la période d'étiage; elles reprennent dès que les eaux commencent à monter. La plupart des poissons paraissent extrêmement sensibles aux varia-tions de niveau, dans un sens ou dans l'autre. Il suffit d'une remontée accidentelle de quelques centimètres à la décrue pour arrêter la progression d'un banc d'*Alestes leuciscus*. Les pêcheurs indigènes sont d'ailleurs unanimes à reconnaître que toute perturbation dans la montée ou la baisse regulière des eaux influe grandement sur la marche des migrateurs qu'ils capturent avec leurs engins. Mais le mécanisme même des migrations longitudinales et leur déterminisme, certainement complexes et liés pour chaque espèce à un rythme in-terne autant qu'aux facteurs externes, nous échappent.

Les migrations latérales sont le fait soit d'adultes en quête de lieux de ponte ou de nourriture, soit d'alevins ou de jeunes en quête d'espace vital. Les poissons de grande taille s'éloignent peu des endroits profonds, lit mineur, mares permanentes, „marigots'' et

dépressions noyées sous plusieurs mètres d'eau. Il n'y a d'exceptions que pour la ponte elle-même; on voit alors des *Clarias anguillaris* et des *Heterotis niloticus* s'engager dans des passages où il n'y a pas plus de 20 centimètres d'eau. Au contraire, les alevins et les espèces de petite taille n'ont pas besoin en général d'une grande profondeur; les eaux non courantes, bien abritées et tranquilles où le plancton se développe abondamment, leur conviennent. Aussi, au maximum de la crue, toute la zone inondée se trouve peuplée de poissons. A la décrue, tous ne partent pas simultanément. Les *Alestes* quittent la plaine dès que le niveau des eaux commence à baisser et en saison sèche on n'en trouve pratiquement pas dans les mares de rétention. Au contraire les *Clarias anguillaris* et les *Polypterus senegalus senegalus* partent les derniers et beaucoup se laissent même surprendre dans des bas-fonds dont ils ne peuvent plus s'échapper; ils finissent par mourir d'asphyxie lorsque le milieu s'assèche complètement; seuls ceux qui ont réussi à gagner des emplacements de mares permanentes peuvent survivre jusqu'à la crue suivante.

En définitive, par les migrations latérales, la population de poissons occupe toutes les eaux disponibles et en utilise au mieux les ressources alimentaires. Elle se disperse au maximum pendant la crue puis se regroupe et se concentre pendant la décrue. On se fera une idée des variations de densité de peuplement qui en résultent si l'on se rappelle que dans le lit mineur du fleuve le niveau monte d'environ 6 mètres au dessus de l'étiage et que la superficie inondée atteint 17.000 km². Par rapport à l'ensemble de la population ichthyologique, les mouvements de migrations latérales pourraient être comparés au flux et au reflux d'une marée qui recouvrirait regulièrement chaque année le secteur deltaïque.

5. ARRÊTS DE CROISSANCE

Un arrêt de croissance prolongé se traduit sur les écailles des poissons par un *annulus*, c'est à dire une ligne de discontinuité dans l'ornementation superficielle entre la région de l'écaille formée avant l'arrêt de croissance et la région formée après. Dans le secteur deltaïque, des *annuli* de ce type sont fréquents; toujours d'une netteté parfaite chez les Characiniformes, ils existent aussi plus ou moins faciles à repérer chez les autres groupes de poissons à écailles. On les a observé chez des carnivores: *Polypterus, Hydrocyon, Lates, Gymnarchus, Parophiocephalus;* des herbivores: *Distichodus, Tilapia zilli;* des limnivores: *Citharinus;* des insectivores: *Ctenopoma*, divers Mormyridés; des planctonophages: *Tilapia galilaea, T. nilotica, Labeo senegalensis;* des poissons à régime mixte, insectivores-grani-

336

vores: *Alestes*, etc. . . . Tous ces poissons subissent donc des arrêts
de croissance linéaire, et le phénomène atteint certainement toutes
les espèces qui vivent plus d'un an, même celles qui sont dépourvues
d'écailles et chez lesquelles il est plus difficile de le mettre en évi-
dence.

Théoriquement, tous les échantillonnages effectués durant la pé-
riode où la croissance est suspendue, devraient donner, pour une
population homogène, des longueurs moyennes ne différant entre elles
que de quantités inférieures à celles que l'on est en droit d'attendre de
l'effet du hasard. Des mesures échelonnées durant une année de-
vraient donc faire apparaitre la ou les saisons durant lesquelles la
croissance linéaire s'arrête. Malheureusement, lorsqu'il s'agit de
populations réparties sur une vaste étendue, l'expérience montre qu'il
est rare de pouvoir prélever tous les échantillons sur un même groupe
d'individus et de façon toujours identique. Les tests d'homogénéité
classiques et notamment la méthode dite analyse de la variance ne
peuvent donc pas servir à mettre en évidence le phénomène qui nous
intéresse. Malgré tout la comparaison des longueurs standard
moyennes calculées sur des échantillons prélevés entre le début de la
décrue et la fin des basses eaux, est assez démonstrative. On trouvera
ci-dessous quelques chiffres relatifs à des *Alestes* de première année,
sans distinction de sexe.

Date et lieu d'échantillonnage	Effectif	Long.st.moyenne
Alestes leuciscus		
30-XII-1950, Ké près Macina	411	64,5 mm
25, 26-II-1950, Diafarabé	438	66,9
5-VII-1950, Diafarabé	825	65,7
Alestes nurse		
9, 10-XI-1950, Ouana	404	104,5 mm
4, 5-I-1951, Markala	490	108,6
13, 14-VI-1951, Diafarabé	434	109,5
Alestes dentex sethente		
8, 9-XI-1950, Ouana	404	128,4 mm
12-V-1951, Diafarabé	425	128,7

Que la croissance linéaire soit arrêtée dès le début de la décrue ou
qu'elle se poursuive encore un peu au delà, elle est de toute façon
nulle durant la période des basses eaux. Elle reprendrait aux eaux
moyennes de crue. On a constaté le début de la formation d'une nou-
velle zone de croissance sur des écailles de *Tilapia zilli* à partir de

juillet. On peut donc conclure d'une façon schématique à la double égalité:

période de hautes eaux = période de croissance active
période de basses eaux = période de croissance arrêtée

Pour certaines espèces, l'arrêt de croissance est aggravé d'une perte de poids assez considérable. Chez *Alestes leuciscus*, le coefficient de condition K = 10^5 P/L³, P étant le poids en grammes et L la longueur standard en millimètres, varie de 2,73 en novembre à 1,88 en juillet. Corrélativement, la teneur en huile extractible par simple ébullition en milieu aqueux, et qui atteignait le chiffre énorme de 27 °/₀ du poids frais en novembre, tombe à 5 °/₀ en juillet. Ces valeurs calculées pour l'ensemble de la population de première année, montrent que les *Alestes leuciscus* subissent à la baisse des eaux une crise qui serait probablement fatale à l'espèce si celle-ci, par un processus adaptatif, n'avait acquis la possibilité d'accumuler rapidement pendant la crue d'importantes réserves adipeuses.

Les *Tilapia zilli* adultes perdent également 10 à 11 °/₀ de leur poids pendant les basses eaux, mais l'allure du phénomène n'est pas la même suivant qu'il s'agit d'individus qui se trouvent dans le lit mi-
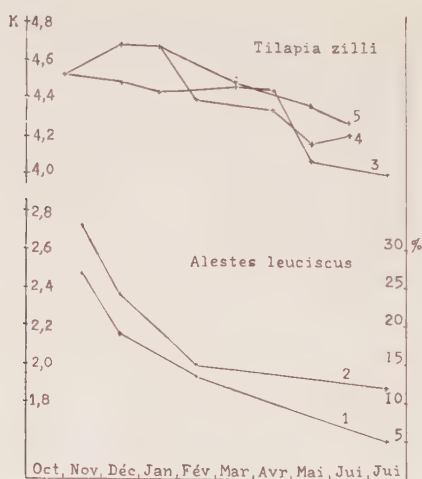

Fig. 4.

1, variations de la teneur en huile, en °/₀ du poids frais (chiffres à droite) chez *Alestes leuciscus*. — 2, variations du coefficient de condition (chiffres à gauche) chez *Alestes leuciscus*. — 3, id. chez *Tilapia zilli* dans le fleuve. — 4, id. chez *Tilapia zilli* dans des mares pauvres. — 5, id. chez *Tilapia zilli* dans une mare un peu plus riche.

neur dès le début de la décrue, ou d'individus qui restent dans la plaine le plus longtemps possible et passent la saison sèche dans des mares de rétention. Dans le fleuve, le coefficient de condition reste compris entre 4,5 et 4,4 de décembre à avril, puis il descend brusquement en mai, probablement par suite des fatigues de la fraye, et n'est plus que de 4,0 en juillet. Dans la plaine, le coefficient de condition augmente jusqu'en décembre—janvier, par suite de la formation de réserves adipeuses, et atteint presque 4,7. Il diminue ensuite, plus ou moins vite suivant la richesse des mares, et atteint 4,2 en mai—juin.

La quantité et la qualité de la nourriture disponible joue certainement un rôle primordial dans les phénomènes d'arrêt de croissance et d'amaigrissement. En ce qui concerne les *Alestes*, il n'est pas douteux que la période des hautes eaux est également celle d'une alimentation riche et copieuse: on trouve les estomacs constamment bourrés de graines et d'insectes. Au contraire à partir de la décrue, les tubes digestifs restent vides ou ne contiennent qu'un peu de phytoplancton. De leur côté les *Tilapia zilli* ne trouvent à manger des herbes en abondance que durant les hautes eaux; c'est cette nourriture uniquement composée de végétaux supérieurs, qui permet aux individus restant dans la plaine, puis dans le lit majeur, jusqu'en décembre—janvier, d'arriver à un état d'adiposité extrême, le coefficient de condition étant voisin de 4,7. Dans le fleuve, l'alimentation est moins riche; elle comprend surtout du phytoplancton et rarement des végétaux supérieurs. Dans les mares elle est franchement mauvaise; les contenus stomacaux ne se composent que d'un peu de phytoplancton dans beaucoup de terre ou de vase.

Toutefois, la nourriture n'est pas seule en cause, car des espèces limivores comme les *Citharinus* ou carnivores comme les *Hydrocyon*, subissent également des arrêts de croissance, bien qu'elles aient à leur disposition, en toute saison, les aliments qui leur conviennent en quantité suffisante. Or, dans le secteur deltaïque, la température moyenne de l'eau, qui reste supérieure à 28° pendant les hautes eaux, descend rapidement à peu près à l'époque de la décrue. L'écart entre le maximum et le minimum des températures moyennes dépasse 8° et pourrait suffire à bloquer la croissance; mais celle-ci devrait alors reprendre lorsque la température remonte, c'est à dire au mois de mai. Jusqu'à présent, aucune observation ne permet de conclure à une reprise de croissance aussi précoce.

Etant donné la pauvreté des eaux en substances minérales, on ne peut éliminer a priori l'hypothèse qu'une substance indispensable pour la croissance normale des poissons fasse défaut à une certaine période de l'année. Il est possible également que la trop forte densité de peuplement qui résulte de la diminution du volume d'eau disponible à la décrue, ait un effet inhibiteur sur la croissance, effet d'autant

plus marqué qu'il s'agit d'un milieu à capacité biogénique faible. Il y a réellement over-stocking aux basses eaux, malgré la pêche qui retire chaque année une quantité de poisson que l'on peut estimer, en l'absence de données statistiques précises, à 40.000 tonnes.

Mais en fait, le problème doit être considéré d'un point de vue plus général et en même temps que tous ceux qui lui sont connexes. La faune ichthyologique du secteur deltaïque doit faire face durant la décrue et les basses eaux à des conditions de vie de plus en plus difficiles à mesure que la saison s'avance. L'assèchement de la zone d'inondation entraine une mortalité considérable chez les jeunes et les petites espèces qui se laissent surprendre par la baisse des eaux avant d'avoir pu rejoindre le lit mineur du fleuve ou les emplacements de mares permanentes. Dans ces dernières, au fur et à mesure que le niveau baisse et que le volume d'eau diminue, une sélection sévère élimine les moins adaptés. Il n'est pas rare de capturer en fin de saison sèche des individus d'une maigreur extrême et, si le niveau baisse de trop, la plupart des espèces disparaissent à l'exception des *Polypteridae* et des *Clariidae*. Dans le lit mineur du fleuve également, les basses eaux constituent une période critique: diminution de la nourriture en quantité et en qualité, variations de température, pauvreté des eaux en substances minérales, trop fortes densités de peuplement, tels sont les principaux facteurs défavorables auxquels les poissons se montrent plus ou moins sensibles. Pour chaque espèce, le problème est donc de subsister jusqu'à la crue suivante, grâce à des réactions d'ordre adaptatif, dont les plus générales sont les migrations, l'arrêt de croissance, l'absence de reproduction et l'utilisation de réserves accumulées pendant les hautes eaux.

Certaines espèces sont même arrivées dans cette voie à des solutions tout à fait originales qui rappellent l'anhydrobiose. *Protopterus annectens*, par exemple, sans chercher à éviter les conséquences du retrait des eaux par une migration latérale, s'enfonce sur place dans le sol encore humide et y attend, à l'état de vie ralentie, la saison des pluies suivante. Ceci lui est possible grâce à sa faculté de s'enfermer dans un cocon parcheminé qui réduit au minimum les risques de déshydratation et grâce à ses poumons capables de respiration aérienne. Dans la région de Diafarabé, *Protopterus annectens* peut rester enkysté huit mois sur douze; on ne le trouve jamais ni dans le fleuve ni dans les mares en saison sèche. Le Cyprinodontidé que nous avons déterminé *Aphyosemion walkeri* ne se rencontre, lui aussi, que quelques mois de l'année dans la région de Diafarabé. Il apparait dans les mêmes biotopes que le Protoptère, c'est à dire dans de petites mares d'eau de pluie qui ne sont pas encore atteintes par les eaux de la crue. Nos observations ne laissent aucun doute sur le fait qu'il s'agit d'oeufs pondus l'année précédente, avant le retrait des eaux, ayant

passé la saison sèche dans le sol et qui ont éclos après les pluies. Ces *Aphyosemion walkeri* seraient donc à rapporter au genre *Notobranchius* et doivent être étroitement apparentés au *Notobranchius gambiensis* (SVENSSON) qui présente les mêmes particularités biologiques dans la zone d'inondation de la Basse Gambie.

Que toutes ces réactions adaptatives au régime d'inondation annuelle dépendent dans une certaine mesure de facteurs internes nous est suggéré par deux observations curieuses concernant l'une *Barbus gambiensis* (= *B. deserti*), l'autre *Protopterus annectens*. JOHNELS (1952) a signalé que des *Barbus gambiensis* rapportés en Suède au mois de novembre et conservés en aquarium dans des conditions aussi constantes que possible, ont néanmoins présenté des arrêts de croissance durant les étés suivants, exactement comme leurs congénères restés en Gambie. Le phénomène ne peut être du qu'à un facteur intrinsèque, caractéristique sinon de l'espèce, du moins de la population dont provenaient les individus observés. Par ailleurs BLANC, d'AUBENTON et PLESSIS (1955) ont constaté qu'un *Protopterus annectens*, ramené de Diafarabé à Paris au mois de septembre et lui aussi conservé en milieu pratiquement invariable, montra en février des signes manifestes de transformation physiologique [1] nécessitant l'enkystement. Que ceci se soit produit au mois de février alors que l'individu en question, resté dans son pays d'origine, se serait enkysté un peu plus tôt, probablement en décembre, ne change rien quant aux conclusions que l'on peut tirer de cette observation, à savoir que le déterminisme de l'enkystement n'est pas du simplement à l'action du milieu. Il resterait à savoir si ces facteurs internes se transmettent intacts ou atténués aux générations suivantes ou s'ils disparaissent totalement. Il y a là un champ de recherches expérimentales qui nécessiteront des observations multiples et prolongées mais dont les résultats pourraient présenter un gros intérêt du point de vue des théories de l'évolution et de la transmission des caractères acquis.

6. COURBES DE CROISSANCE

Le fait que dans le secteur deltaïque les pontes aient lieu à une époque fixe de l'année et que les écailles portent des *annuli* annuels, permet d'évaluer assez facilement l'âge des poissons. On constate que celui-ci est rarement élevé. Les espèces de petite taille ne doivent qu'exceptionnellement dépasser deux ans. Sur des milliers d'*Alestes leuciscus* examinés, nous n'en avons trouvé qu'un très petit nombre

---

[1] Des phénomènes analogues avaient déjà été signalés par BARBOUR (1941), voir JOHNELS et SVENSSON, 1954, p. 143.

dans leur seconde année et aucun de troisième année. Parmi les autres espèces étudiées à ce point de vue, nous avons trouvé comme âge maximum: cinquième année pour *Alestes nurse*, sixième année pour *Tilapia zilli* et *Alestes macrolepidotus*, septième année pour *Alestes dentex sethente* et *A. baremoze*. Il s'agit là de poissons de taille moyenne, ne dépassant pas 40 cm de longueur standard. Les *Lates niloticus*, qui atteignent dans la région considérée ici une longueur standard de 1,50 m, ne dépasseraient pas vingt ans. D'une façon générale, le taux de métabolisme est plus élevé en pays tropical qu'en pays tempéré, ce qui se traduit par une durée de vie plus courte, une croissance plus rapide et une maturité sexuelle plus précoce.

Les courbes de croissance concernant l'ensemble d'une espèce dans les conditions naturelles, n'ont encore été déterminées que dans un petit nombre de cas. Mais quelques considérations d'ordre général peuvent déjà être dégagées des résultats obtenus. La croissance des mâles est souvent différente de celle des femelles; suivant les genres, les premiers ont une croissance plus rapide ou au contraire plus lente et atteignent des tailles maxima plus élevées ou plus faibles. Chez les *Alestes*, les mâles sont toujours plus petits que les femelles, c'est l'inverse chez les *Tilapia zilli*, ainsi qu'il apparait dans le tableau suivant:

	Longueur standard maxima observée	
	mâles	femelles
Alestes leuciscus	89 mm	97 mm
Alestes dentex sethente	332 mm	362 mm
Alestes baremoze	252 mm	272 mm
Tilapia zilli	250 mm	230 mm

A âge égal, les longueurs moyennes diffèrent aussi suivant les sexes. Lorsque la maturité sexuelle est normalement atteinte la première année, l'écart est déjà notable à la fin de la première période de croissance. Ainsi chez les *Alestes leuciscus*, on trouve comme longueur standard moyenne 63,4 mm pour les mâles et 67,2 mm pour les femelles. Lorsque la maturité sexuelle n'est atteinte que la seconde année, l'écart n'est pas notable au bout de la première période de croissance; il le devient seulement au bout de la seconde. C'est le cas des *Alestes dentex sethente*, des *A. baremoze* et aussi des *Tilapia zilli* bien qu'un certain nombre d'individus de cette dernière espèce soient déjà aptes à se reproduire au bout d'un an. Par la suite les différences vont en s'accentuant au fur et à mesure que l'âge augmente, comme on le voit dans le tableau suivant:

	Longueurs standard moyennes en mm.					
	A. dentex sethente		A. baremoze		Tilapia zilli	
	♂	♀	♂	♀	♂	♀
1ere année	128,7		78,7		95,2	95,3
2eme année	201,8	207,9	177,3	182,3	157,9	150,4
3eme année	235,2	246,5	198,0	208,4	190,6	179,0
4eme année	253,7	276,5	210,3	223,6	207,4	191,3
5eme année	267,5	294,0	218,6	234,4	214,2	205,6
6eme année	285,7	315,4	226,6	243,0		

Si l'on porte les longueurs moyennes correspondant aux différents âges, sur un diagramme en coordonnées logarithmiques, on constate que pour chaque espèce et chaque sexe les points sont alignés à partir de trois ans. Mais ces droites ont des pentes nettement plus faibles que celles qui joignent les points correspondants de un et deux ans. Ceci veut dire que la croissance est plus lente chez les adultes que chez les immatures. On ne peut donc représenter la croissance par une seule formule; il est nécessaire d'en utiliser deux de la forme
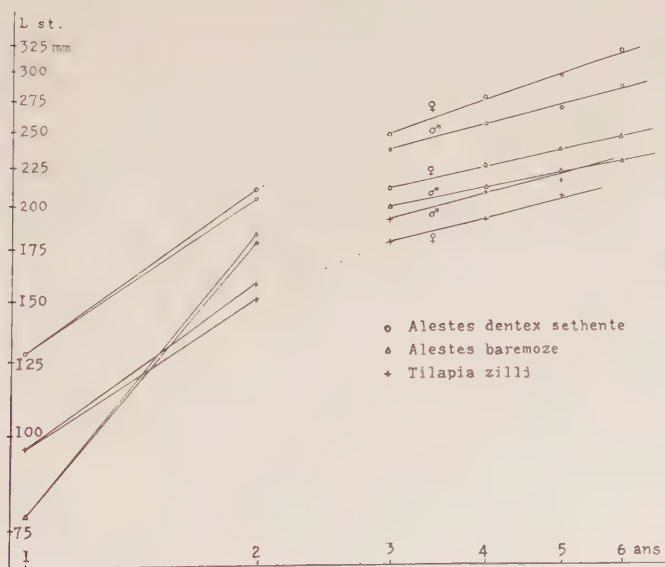

Fig. 5.

Courbes de croissance en coordonnées logarithmiques d'*Alestes dentex sethente*, d'*Alestes baremoze* et de *Tilapia zilli*.

Long.st. $= A \times N^k$, l'une valable pour N $= 1$ et 2 ans, l'autre pour N $= 3,4, \ldots$ ans. Ainsi, pour *Alestes dentex sethente*, on pourra représenter la croissance par les formules:

$L = 128,7 \times N^{0,649}$ (N $= 1,2$) et $L = 175 \times N^{0,268}$ (N $= 3,4 \ldots$) pour les mâles.

$L = 128,7 \times N^{0,692}$ (N $= 1,2$) et $L = 163 \times N^{0,370}$ (N $= 3,4 \ldots$) pour les femelles.

7. ADAPTATIONS RESPIRATOIRES

Les adaptations d'organes à rôle respiratoire que l'on peut observer chez les poissons du delta central nigérien sont les unes transitoires (structures juvéniles, au moins fonctionnellement), les autres permanentes (structures adultes). Parmi les premières, le cas le plus simple est celui des filaments branchiaux des jeunes *Heterotis* et *Gymnarchus niloticus*, qui dépassent longuement à l'extérieur de la cavité branchiale. Les alevins qui présentent ces filaments sont relativement volumineux à l'éclosion puisque les oeufs ont un diamètre de 2,5 mm chez *Heterotis* et 9—10 mm chez *Gymnarchus;* ces oeufs sont déposés en eau stagnante, dans des nids bien abrités au milieu des herbes mais non ombragés, où la température de l'eau peut facilement dépasser 33° dans la journée; aussi est-il vraisemblable que les alevins avant de pouvoir nager normalement, se trouvent exposés à souffrir de taux d'oxygène dissous assez bas. Ces filaments branchiaux régressent d'ailleurs assez vite et reprennent des dimensions normales, c'est à dire ne sont plus visibles extérieurement, lorsque les jeunes poissons quittent leur nid. Il s'agit donc bien de structures juvéniles qui doivent faciliter la respiration à un stade du développement où des branchies de type habituel risqueraient d'être insuffisantes.

Les jeunes *Polypterus* possèdent une véritable branchie externe, adventice sur l'opercule, et composée d'un axe charnu portant sur les bords une frange de filaments. Cette branchie apparait très tôt au cours de l'organogenèse, avant l'ouverture des fentes branchiales embryonnaires. Elle cesse d'être fonctionnelle, régresse et disparait totalement au cours de la première année; on n'en trouve même plus trace chez l'adulte. Cette régression n'est pas directement liée à la taille du poisson comme on l'avait supposé autrefois. A Diafarabé, de jeunes *Polypterus senegalus senegalus* de 38 à 45 mm de longueur standard, capturés le 13 décembre, montrent déjà des branchies externes en régression très avancée, alors que d'autres de 49 à 73 mm, capturés le 25 novembre en ont encore de bien développées. En fait, la régression débute avec la décrue; elle est achevée aux basses eaux. Au mois de mars, les jeunes *Polypterus senegalus*, quelle que soit leur taille,

ne montrent plus aucune trace de branchies externes. Les mêmes phénomènes s'observent chez *Polypterus bichir lapradei* et *P. endlicheri endlicheri*, mais les jeunes de ces deux dernières espèces atteignent à âge égal des tailles très supérieures à celles des *P. senegalus senegalus*, de sorte que l'on peut rencontrer des individus mesurant jusqu'à 250 mm de longueur standard et portant des branchies externes bien développées. Il serait cependant inexact de conclure que la disparition de ces organes juvéniles, parce qu'elle se produit en même temps que l'arrêt de croissance, procède des mêmes causes, car on l'observe chez tous les *Polypteridae*, quels que soient le milieu et la région où ils vivent, et non seulement chez ceux du secteur deltaïque.

Les jeunes *Protopterus annectens* possèdent aussi de véritables branchies externes, au nombre de quatre, puis trois, comme les têtards d'Amphibiens. Chez des jeunes de 35 mm de longueur totale, au début de septembre, les filaments sont bien développés; ils sont nettement en régression chez d'autres mesurant de 40 à 52 mm et capturés en fin novembre. Il y aurait donc analogie avec les faits signalés précédemment au sujet des Polyptères; mais chez les Protoptères, les filaments seuls disparaissent et les axes charnus qui les portaient subsistent encore après le premier enkystement. Des adultes de grande taille, certainement âgés de plusieurs années, les possèdent encore. Naturellement, ces vestiges de branchies externes juvéniles ne sont plus fonctionnels.

Parmi les adaptations respiratoires permanentes, la plus remarquable est celle de la vessie aérienne de *Protopterus annectens*. Cet organe est en fait transformé en un véritable poumon, capable d'assurer une respiration strictement aérienne pendant toute la saison sèche; il s'agit donc là d'une adaptation parfaite à la vie dans une région tour à tour inondée et asséchée. Les *Polypterus* possèdent aussi une vessie aérienne susceptible d'absorber l'oxygène de l'air, mais moins spécialisée anatomiquement et histologiquement que celle des *Protopterus;* elle ne peut que supplémenter dans une certaine mesure la respiration branchiale aquatique. En effet, si *Polypterus senegalus senegalus* peut vivre encore dans la boue liquide des fonds de mare en voie d'assèchement, il ne semble pas capable de mener une vie proprement aérienne. Les *Clariidae*, *Clarias* et *Heterobranchus*, possèdent un organe respiratoire accessoire d'une efficacité supérieure; il se présente sous la forme d'arborescences, rappelant un chou-fleur et logées dans une cavité au dessus des branchies. Le sang s'y oxygène à partir de l'air atmosphérique. Les *Clarias* peuvent se passer d'eau pendant un laps de temps assez long, soit qu'ils s'enfoncent dans la boue ou la terre humide des fonds de mare asséchés, soit qu'ils se déplacent sur le sol pour passer d'un point d'eau à un autre. Enfin, signalons que *Ctenopoma petherici* possède un organe respiratoire

accessoire formé d'une lamelle plissée et comme tuyautée, logée dans une cavité suprabranchiale, et que *Parophiocephalus obscurus* possède seulement une cavité suprabranchiale. Les structures de ces organes sont assez différentes, mais la convergence est telle que les *Anabantidae* et les *Ophiocephalidae* ont longtemps été réunis dans le groupe artificiel des *Labyrinthidae*. *Ctenopoma petherici* et *Parophiocephalus obscurus* appartiennent à la faune caractéristique des mares. Il semble bien que leurs organes suprabranchiaux, comme celui des *Clariidae* et comme la vessie aérienne des *Polypterus*, représentent des palliatifs divers et plus ou moins heureux aux dangers d'asphyxie dans les eaux tropicales stagnantes. Il resterait à démontrer dans quelle mesure ils sont efficaces, compte tenu de la capacité de fixation de l'oxygène par les pigments respiratoires du sang.

RÉSUMÉ ET CONCLUSIONS

Le delta central nigérien ou secteur deltaïque de la zone d'inondation du Niger moyen, est situé dans une région à climat tropical soudanien, caractérisé par une longue saison sèche et une saison des pluies assez courte. L'influence des pluies locales est négligeable sur la crue annuelle du fleuve; celle-ci est due uniquement aux précipitations sur le bassin versant du Haut Niger et de ses affluents. Au mois d'octobre, le secteur deltaïque est recouvert par une nappe d'eau de 17.000 km², soit la moitié du lac Tanganika en superficie. Au mois de mai, il ne reste que quelques mares et le fleuve, sans profondeur, a un débit 25 fois moins important qu'en période de crue. Les eaux sont très peu minéralisées, pauvres au point de vue biogénique. Cependant la faune ichthyologique y est riche et variée, comparable à celle du bassin du Nil; elle présente des particularités biologiques remarquables et qui sont autant d'adaptations aux conditions de vie difficiles que les poissons subissent pendant la période des basses eaux.

1) A part de rares exceptions, la reproduction débute en fin de saison sèche (*Tilapia zilli*) ou le plus fréquemment aux eaux moyennes de crue; elle est terminée au début de la décrue.

2) Beaucoup d'espèces effectuent des migrations saisonnières, soit longitudinales, dans le lit mineur du fleuve, soit latérales, du lit mineur vers le lit majeur ou la plaine d'inondation et vice versa. Les migrations anadromes sont surtout bien connues: la plupart n'ont rien à voir avec la reproduction; leur déterminisme complexe n'apparait pas clairement.

3) Tous les poissons subissent un arrêt de croissance annuel durant la période des basses eaux; pour certains même il y a perte de poids. *Protopterus annectens* passe la période difficile des basses eaux

enkysté; *Aphyosemion* (*Nothobranchius*) *walkeri* pond des oeufs durables qui supportent une dessication prolongée du milieu où ils ont été déposés.

4) Les courbes de croissance des populations naturelles montrent que mâles et femelles obéissent souvent à des lois de croissance différentes. Dans les cas étudiés, la croissance est considérablement ralentie à partir de la maturité sexuelle.

5) Nombre d'espèces présentent des adaptations respiratoires, soit juvéniles: filaments branchiaux prolongés (*Hetcrotis*, *Gymnarchus*), ou véritables branchies externes (*Protopterus*, *Polypterus*); soit adultes: poumon (*Protopterus*), vessie aérienne respiratoire (*Polypterus*), organes respiratoires accessoires suprabranchiaux (*Claridiae*, *Ctenopoma*, *Parophiocephalus*).

RÉFÉRENCES BIBLIOGRAPHIQUES

BLACHE, J. et GOOSSENS, J. - 1954 - Monographie piscicole d'une zone de pêche au Cambodge, *Cybium*, 8, 49 p., 9 pl.

BLANC, M., DAGET, J. et D'AUBENTON, F. - 1955 - Recherches hydrobiologiques dans le bassin du Moyen Niger, *Bull. IFAN*, XVII, 3, 679—754, 29 fig., 8 pl.

BLANC, M., D'AUBENTON, F. et PLESSIS, Y. - 1955 - Note préliminaire sur l'enkystement de *Protopterus annectens* (OWEN 1839), *Bull. Mus. nat. Hist. nat.*, XXVII, 3, 193—195.

DAGET, J. - 1952 - Biologie et croissance des espèces du genre *Alestes*, *Bull. IFAN*, XIV, I, 191—225, 8 fig.

——— 1954 - Les Poissons du Niger supérieur, *Mémoires IFAN*, Dakar, 36, 391 p., 141 fig.

——— 1956 - Recherches sur *Tilapia zilli* (GERV.), *Bull. IFAN*, XVIII, sér. A, 1, 165—223, 8 fig.

GRAS, R. - 1956 - Contribution à l'étude des *Alestes dentex* du Niger supérieur, *Bull. IFAN*, XVIII, sér. A, 2, 532—538, 1 fig.

JOHNELS, A. G. - 1954 - Notes on fishes from the Gambia River, *Ark. f. Zool.*, VI, 17, 327—411, 19 fig.

JOHNELS, A. G. et SVENSSON, G. S. O. - 1954 - On the biology of *Protopterus annectens* (OWEN), *Ark. f. Zool.*, VII, 7, 131—164, 13 fig.

SANDON, H. - 1950 - An illustrated guide to the freshwater fishes of the Sudan, *Sudan Notes and Records*, 25, 61 p., 14 pl.

SVENSSON, G. S. .O - 1933 - Freswater fishes from the Gambia River, *Kungl. Sv. Vet. Handl.*, 12, 3, 102 p., 28 fig., 8 pl.

WELMAN, H. - 1948 - Preliminary survey of the freshwater fisheries of Nigeria Lagos, 71 p., 11 pl.

Beiträge zur Limnologie und Rädertierfauna Ungarischer Natrongewässer

von

T. Nógrádi

Manche Teile der ungarischen Tiefebene zeigen eine ganz spezielle Beschaffenheit was die Bodenkunde und die regionallimnologischen Verhältnisse betrifft. Der Boden dieser Gegenden ist meistens strukturlos, lehmig, wenig oder gar unfruchtbar. An vielen Stellen kristallisiert Na_2CO_3 und $NaHCO_3$ aus dem Boden. Das Bodenwasser-Niveau ist meistens hoch. Die kaum 1 Meter tiefen Seen und Teiche sowie auch die zahllosen Tümpel sind meist vorübergehend, im Sommer sind sie — mit Aussnahme der tiefsten Stellen — fast immer ausgetrocknet, oder führen nur in einigen Pfützen beinahe Rahmdickes Wasser von extrem hohem Gehalt an Salzen, hauptsächlich Na_2CO_3 oder $NaHCO_3$. Das Wasser ist durch kolloidalen Lehm und ausgeflockte Ca-Salze immer sehr stark getrübt, die Durchsichtigkeit beträgt manchmal nur 1—2 cm. Das Wasser ist darum von typisch hellgrauer Farbe. Deswegen ist der Temperaturgradient der Teiche überraschend gross. An der Oberfläche folgt die Wassertemperatur schnell den Änderungen der Lufttemperatur, ist also grossen Schwankungen unterworfen. In den „tieferen" Wasserschichten und am Boden ist sie aber oft um 4—6° C. niedriger und zeigt grössere Konstanz. Starker Wind ruft leicht schnelle Denivellation der seichten Wassermenge hervor.

Ich untersuchte manche Natronteiche und Tümpel in der Nähe des Städtchens FÜLÖPSZÁLLÁS (zwischen der Donau und der Theiss, 80 Km von BUDAPEST entfernt) wo sehr viele solcher Gewässer zu finden sind (Abb. 1.). Diese erstrecken sich teilweise zwischen Ackerland, teilweise an Soda- und Moorgelände. Es gibt hier noch eine Menge Teiche und Tümpel, die durch ihr klares Wasser leicht von den typischen Sodagewässern zu unterscheiden sind.

Die chemischen Analysen (Tab. 1.) zeigen, dass es sich um Na^+ — HCO'_3 Gewässer handelt. CO''_3 und freies CO_2 sind nicht vorhanden, die Teiche sind also nach dem System von R. MAUCHA(5) in den

α-*limno* Typ einzureihen. Der Gehalt an Ca^{++}, Mg^{++}, SO$_4''$ und CI$'$—Ionen ist ganz gering. Das pH variiert zwischen 8.0 und 8.5. Die klares Wasser führenden Teiche und Tümpel zeigen grundsätzlich denselben Chemismus, sind also auch Natrongewässer, sie haben aber einen wesentlich höheren Gehalt an Ca^{++} und SO$_4''$ als die

Abb. 1.
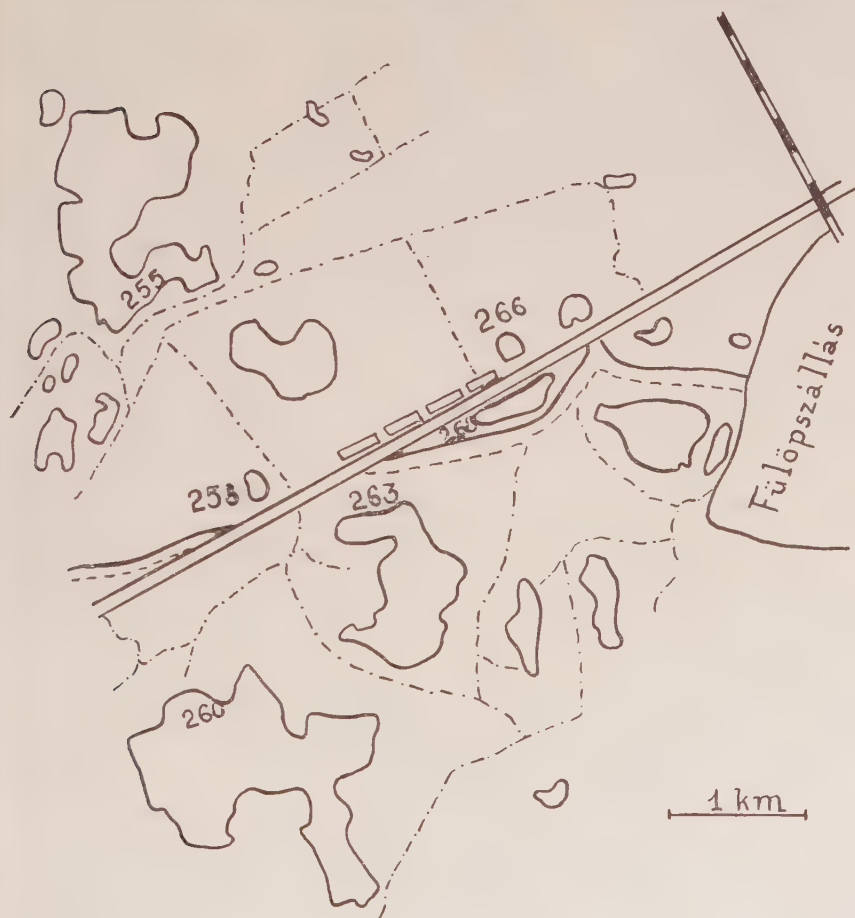Umgebung des Städtchens Fülöpszállás (Ungarn)

typischen grauen Teiche. Das lässt vermuten, dass die Ca-Salze die Ausflockung und Sedimentierung des Lehm-Kolloides und dadurch klares Wasser verursachen. Interessanterweise sind die beiden Typen manchmal nur einige Meter von einander entfernt.

Die Ergebnisse der zoologischen Untersuchungen sind aus der Tabelle II. zu entnehmen. Mit Kreuzen ist die Häufigkeit des Vor-

	Grauwasserteiche			Klarwasserteiche		
	255	260	263	258	266	268
Wassertemperatur	14°	14°	15°	16°	18°	18°
Durchsichtigkeit cm.	0—1	2—4	3—5	30	20	30
Alkalität, Wartha°	16°	10°	8°	8°	17°	6°
Carbonathärte	47,5°	27.5°	22.4°	22.4°	50.1°	16.8°
Gesamthärte	4°	4°	5°	6°	6°	6°
Ca-Härte	3°	3°	3°	5°	6°	4°
Na⁺ mg/lit.	376	203	148	138	366	91
aequiv.%	93.0	87.0	79.0	74.0	89.0	65.0
Ca⁺⁺ mg/lit.	21.4	21.4	25.0	35.7	42.8	28.5
aequiv.%	6.0	10.5	14.6	21.7	11.0	23.3
Mg⁺⁺ mg/lit.	4.3	4.3	6.5	4.3	∅	8.7
aequiv.%	2.0	3.5	6.4	4.3	∅	355
HCO′₃ mg/lit.	980	590	470	470	106	355
aequiv.%	90	95	91	95	96	95
Cl′ mg/lit.	62	18	26	12	19	7
aequiv.%	9.8	5.0	9.0	4.0	3.0	3.3
SO₄″ mg/lit.%	2	∅	∅	4	7	5
aequiv.%	0.2	∅	∅	1.0	0.9	1.7

Bemerkung: Die Numerierung der Teich bezieht sich auf Abb. 1. Es sind die Teiche, die im April einer ausführlichen chemischen Analyse unterworfen wurden, und nur als Beispiele dienen. Die biologischen Untersuchungen sind an viel mehr Teichen und Tümpeln unternommen worden. Die angegebenen Aequivalenten-Prozente sind nach der Methode von MAUCHA (5) berechnet, und dienen zu der graphischen Darstellung in der Form von Sterndiagrammen.

kommens angedeutet, aber immer auf die Gesamtheit der untersuchten typischen (grauen) und klaren Natronteiche bezogen.

Die Cladoceren und Copepoden dieser Gewässer, sowie ihre ausführliche limnologische Beschreibung behandeln wir an anderem Orte (siehe 7.). Hier sei nur kurz erwähnt, dass die Entomostraken eine bessere Möglichkeit zur Beurteilung typischer Natrongewässer-Bewohner bieten als die Rotatorien. Unter den Cladoceren (31 Arten) sind *Daphnia Atkinsoni* und *D. psittacea*, *Moina brachiata* und *M. rectirostris* sowie *Macrothrix hirsuticornis* die charakteristischen Leitformen. Die Vertreter der Copepoden sind auch zahlreich (14 Arten). Hier spielt *Arctodiaptomus spinosus* eine absolute Leitrolle; er ist überall und in grosser Menge zu finden. Häufig ist noch *A. Wierzejskii*, und ziemlich typisch *Hemidiaptomus amblyodon* und *Lovenula Alluaudi*. Die Cyclopiden spielen keine grosse Rolle.

Die Rotatorienfauna ist ziemlich reich, es wurden 52 Arten und 6 Varietäten gefunden. Die Mehrzahl der Arten ist kosmopolitisch und darum näherer Besprechung nicht wert. Einige sind aber entwe-

der neu oder in tiergeographischer Hinsicht interessant; darum be-
handeln wir sie eingehender. Es ist zu bemerken, dass unsere Unter-
suchungen nur die Frühlings- und Frühsommerfauna (April-Juni)
umfassen.

II. TABELLE

	4.IV.		25.IV.		24.V.		1.VII.	
	a.	b.	a.	b.	a.	b.	a.	b.
Rotatoria:								
Rotaria tardigrada Ehrb.								
Habrotrocha sp.								
Notommata najas Ehrb.								
„ aurita O. F. M.								
tura aurita Ehrb.								
Cephalodella forficula Ehrb.								
„ gracilis Ehrb.								
„ catellina O. F. M.								
„ ventripes Dix.-Nutt.								
„ gibba Ehrb.								
Rhinoglena frontalis Ehrb.								
Brachionus capsuliflorus var. brevispinus								
„ „ var. Entzii Francé								
„ „ „ „ f. convergens n.f.								
„ „ „ rhenanus Laut.								
„ urceus L.								
„ rubens Ehrb.								
„ Leydigi var. tridentatus Sern.								
„ Novae-Zelandiae var. hunga-ricus n. var.								
Keratella quadrata O. F. M.								
„ „ var. brevispina Gosse	+++							
„ „ var. valga Ehrb.								
„ cochlearis Gosse								
Notholca striata Ehrb.								
„ acuminata Ehrb.								
Anuraeopsis fissa Gosse								
Mytilina spinigera Ehrb.								
„ bicarinata Perty								
„ ventralis brevispina Ehrb.								
„ mucronata O.F.M.								
Euchlanis dilatata Ehrb.								
Lecane brachydactyla Stenr. (?)								
„ ichthyoura And.-Shep.								
„ luna O.F.M.								
„ sinuosa n.sp.								

	4.IV.		25.IV.		24.V.		1.VII.	
	a.	b.	a.	b.	a.	b.	a.	b.
Monostyla lunaris Ehrb.					+	+	+	+
„ bulla Gosse	+				+			+
„ closterocerca Schm.		+						+
Lepadella patella O.F.M.	+	+		+	+	+		
„ rhomboides Gosse		+		+				
„ amphitropis Harring	+	++						
Lophocharis oxysternon Gosse		+		+				
„ salpina Ehrb.		+		+		+		
Squatinella lamellaris O.F.M.								+
Colurella adriatica Ehrb.	+							
Diurella brachiura Gosse		+						
Trichocerca carinata O.F.M.								+
„ stylata Gosse (?)					+			
Synchaeta pectinata Ehrb.								+
„ oblonga Ehrb.				+				+
Polyarthra vulgaris Carlin	+			+				+
„ minor Voigt				+				+
Filina longiseta Ehrb.		+	+	+				+
„ cornuta Gosse		+						+
Pedalia mira Hudson				+				+
Asplanchnopus syrinx Ehrb.					+			
Testudinella sp.		+						
Pompholyx sulcata Hudson		+						
Cladocera:								
Daphnia magna Str			++	+	+	+	++	
„ pulex de Geer			+	+			++	
„ longispina longispina O.F.M.			+	+		+	++	
„ „ caudata G. O. Sars				+				
„ „ hyalina Leydig			++		+			
„ cucullata incerta Rich.	+							
„ psittacea Baird	+		++	+	+	+		
„ Atkinsoni Baird	+++	+	++	+	+			
Ceriodaphnia rotunda G. O. Sars				+				
„ quadrangula O.F.M.				+				
„ megops G. O. Sars								+
Scapholeberis mucronata O.F.M.					+			
„ aurita Fisch				+	+			
Simocephalus vetulus O.F.M.					+		+	
„ exspinosus Koch					+			
Diaphanosoma brachyurum Liévin		+			+		+++	
Moina rectirostris Leydig	+		+++	+	+		+++	
„ brachiata Jur.		+	+		+++	+		
Macrothrix rosea Jur.						+	+	
„ laticornis Jur.					+	+	+	
„ hirsuticornis Norm.-Brad.	+++	+	+	+	+	+	+	

	4.IV.		25.IV.		24.V.		1.VII	
	a.	b.	a.	b.	a.	b.	a.	b.
ona quadrangularis O.F.M.	+	+	+	+	+	+		
,, costata G. O. Sars			+	+				
,, guttata G. O. Sars				+				
,, rectangula G. O. Sars							+	
,, affinis Leydig	+							
,, tenuicaudis G. O. Sars				·				
onella nana Baird						+		
ydorus sphaericus O.F.M.	–	+	+	+ +		+		I +
,, ovalis Kurz				+		+	+	
,, latus G. O. Sars	+	+		+	+	+ +	+	
pepoda:								
(Arctodiaptomus) spinosus Daday	+ +	+	+ + +	+ + +	+ +	+	+ + +	+ +
,, Wierzejskii Rich.	+ +	+ +	+	+	+ +	+		
,, bacillifer Koelb ★	+	+		+	+		+	
(Hemidiaptomus) amblyodon Marenz				+		+		
(Eudiaptomus) gracilis G.O.S.				+				
(Allolovenula) Alluaudi Gu. & Rich.				+		+		
(Cyclops) strenuus Fisch.			+	+		+	+	–
(Diacyclops) bisetosus Rehb.	+	+					+	
,, bicuspidatus Claus				+				
,, languidoides Lillj.	+							
,, nanus G.O.S.						+		
(Acanthocyclops) vernalis Fisch.	+	+	+	+	+	+		
(Megacyclops) viridis Jur.	+					+	+	
nthocamptus staphylinus Jur.	+	+		+	+	+	+	

Zeichenerklärung: a. = Grauwasserteiche
b. = Klarwasserteiche

★ Die Art ist nach der persönlichen Mitteilung von Herrn J. Ponyi höchst-
wahrscheinlich nicht *D. bacillifer*, sondern seine neue Art *D. natronophilus*.
Die echte *bacillifer* scheint in den ungarischen Natronteichen selten zu sein.

SYSTEMATISCHER TEIL

Brachionus capsuliflorus var. Entzii (Francé) (Abb. 2.)
   Die bekannte Art war häufig zu finden. Es bevorzugte eher typische
Natronteiche. Die Länge der Exemplare variierte zwischen 320—
400μ, ensprechend der üblichen Angaben.
Brachionus capsuliflorus var. Entzii f. convergens n.f. (Abb. 3.)
   Fast immer dort, wo die Stammvariation auftrat, war auch eine
interessante Form zu finden, die, wie aus der dritten Abbildung

ersichlich ist, grundsätzlich von dieser abweicht. Der vordere Panzerumriss entspricht vollkommen der normalen Varietät, die beiden medialen Dornen sind ziemlich kurz. Der hintere Teil des Panzers ist aber in zwei kurze Spitzen ausgezogen. Diese sind in der Linie der submedianen Dornen und sind 120—130 μ von einander entfernt. Zwischen ihnen ist eine relativ enge und ziemlich tiefe Einbuchtung. Der Panzer ist darum birnförmig, im zweiten Drittel am breitesten, ausgebaucht und leicht gekörnt. Die Körpermasse entsprechen der Stammvarietät.

Abb. 2. Brachionus
capsuliflorus var. Entzii (Francé).

Abb. 3. Brachionus capsuliflorus
var. Entzii f. convergens n.f.

Brachionus Novae-Zelandiae (Morris), 1913. (Abb. 4, 5.)

MORRIS (6) beschrieb aus Oamaru, Neu-Seeland ein sehr sonderbar gestaltetes Rädertier als *B. variabilis var. Novae- Zelandiae*(Abb. 4.), welches in AHLSTRÖM'S Brachionus-Monographie (1) als selbstständige Art behandelt wird. Das Tier ist unseres Wissens nach noch nicht wiedergefunden worden.

In 1932, bei der grosszügigen Bearbeitung der süd-afrikanischen „Pfannen-Teiche" (pans) durch HUTCHINSON, PICKFORD und SCHUURMANN (3) ist eine verwandte Form aufgetaucht, und wurde von D. L. BRYCE, dem Bearbeiter der Rotatorien als *B. capsuliflorus var. Novae-Zelandiae* (BARHAM) (?) bestimmt. Die Abbildung und Beschreibung des Tieres ist aber nur in AHLSTRÖM'S erwähntem Werk zu finden. Diese Form, die in Süd-Afrika (Chrissie-Bezirk) in dem Eilandspan und Stormberg-Dam gefunden wurde, ist aber von der neuseeländischen Art sehr abweichend (Abb. 5.) Es ist darum sehr überraschend, dass sie mit der Stammform identisch genommen wurde, und bei AHLSTRÖM auch nicht als Varietät beschrieben wird, da er die zwei Formen separat behandelt, und die sehr auffallenden Unterschiede genau herausarbeitet. In der *Brachionus*-Monographie von BARTOS (2) ist nur die MORRIS'sche Stammform erwähnt. Wir

354

halten es darum angebracht, die von HUTCHINSON et al. gefundene Art als *Brachionus Novae-Zelandiae var. africanus nom. nov.* zu benennen.
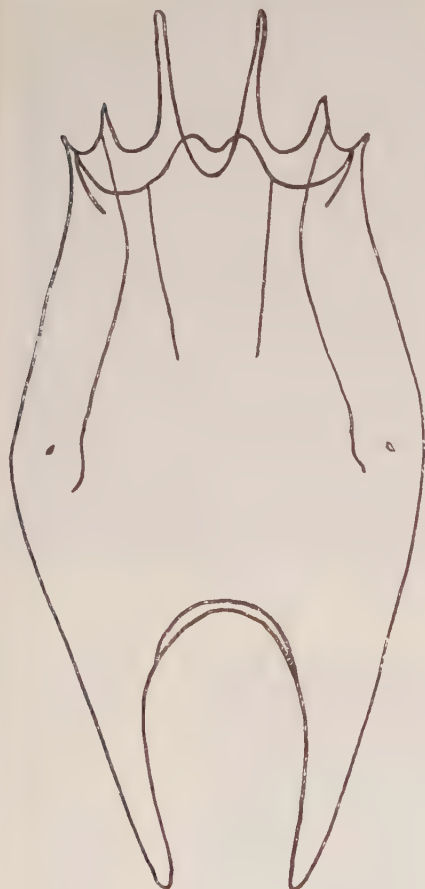

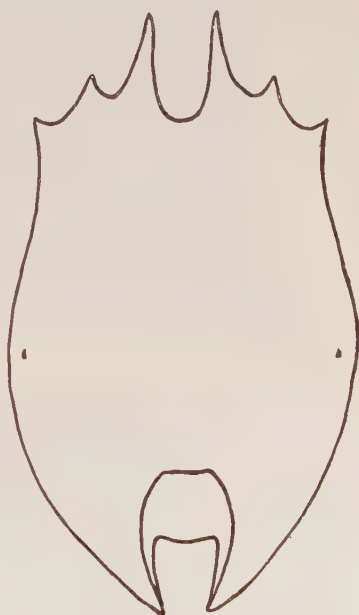Abb. 4. Brachionus Novae-Zelandiae (MORRIS). Stammform. (Nach AHLSTRÖM (1)).

Abb. 5. Brachionus Novae-Zelandiae (MORRIS) var.africanus nom. nov. (Nach AHLSTRÖM (1)).

Brachionus Novae-Zelandiae var. hungaricus n. var. (Abb. 6—9.)

In mehreren der untersuchten Natronteichen fanden wir zu unserer grossen Überraschung eine *Brachionus*-Art, die nur zu *B. Novae-Zelandiae* zu stellen war. Die eingehende Untersuchung der gefundenen Exemplare bestätigte diese Auffassung[*] und zeigte, dass

---

[*] Sie wurde ursprünglich von Herrn KURT WULFERT (Bad-Lauchstädt) brieflich aufgeworfen, wofür ich ihm auch an dieser Stelle herzlichen Dank sagen möchte.

wir es mit einer neuen Varietät zu tun haben. Diese, wie es aus der sechsten Abbildung zu sehen ist, bildet einen Übergang zwischen der Stammform und var. africanus.
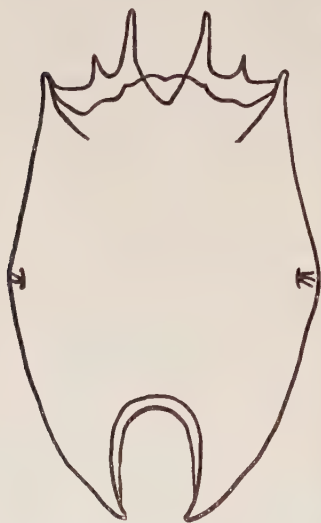

Abb. 6.
Brachionus Novae-Zelandiae
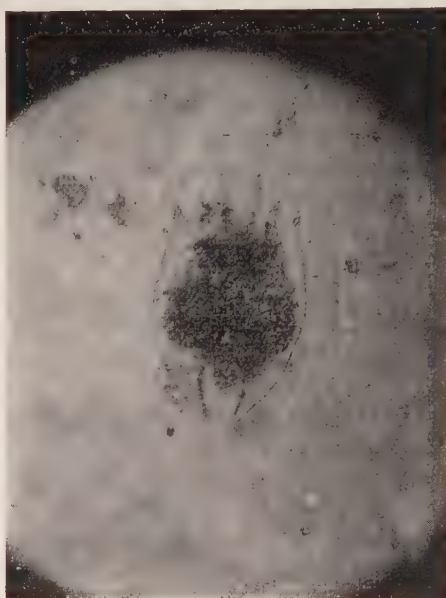var. hungaricus n. var.

Abb. 7.

Das Tier ist von ovaler Form, in der Mitte seitlich ein wenig eckig gewölbt. Die dorsalen Stirnrand-Dornen sind der Stammform ähnlich, der Ausschnitt zwischen den beiden medianen Dornen ist aber eher V-förmig. Der ventrale Panzerrand (an der Abb. 8 besonders gut zu sehen) läuft eigenartig gewellt, mit zwei deutlichen, nach aussen geneigten spitzen lateralen Dornen. Die kaudalen „Dornen", die eher als Rand der grossen Fussöffnung aufzufassen sind, machen 23 % der totalen Körperlänge aus (bei der Stammform mehr als 30 %). Der dorsale und ventrale Ausschnitt der Fussöffnung ist beinahe gleich gross, halboval, ganz abweichend von dem abgestumpftem Oval der var. africanus. Die Tastborsten befinden sich am breitesten Punkt des glatten Panzers.

Bei einem jungen Exemplar (Abb. 9.) sind die Formen des noch weichen Panzers noch nicht ganz ausgebildet, die Fussöffnung ist schmaler, sackartig.

Die Tiere wurden Ende April in mehreren Natronteichen gefunden. Das Auftauchen dieser sehr seltenen Art in Europa — wenn auch in einer Varietät — ist durchaus überraschend. Die von uns untersuchten Soda-Teiche sind aber (nach — nach heutiger Auffassung — lückenhaften chemischen Angaben von Hutchinson et al. urteilend)

den südafrikanischen „Pfannen" ziemlich ähnlich. Dort ist die Durchsichtigkeit auch gering (21.5 cm), Wasserfarbe bräunlich-grau, pH: 9.0, im Wasser ist kolloidaler Lehm suspendiert (vergleiche unsere Tabelle I.)

Körpermasse: Totale Länge 192—205 μ, maximale Breite 115—120 μ, Stirndornen 8, 10, 31 μ, Fussöffnung 42 μ. Die neue Varietät
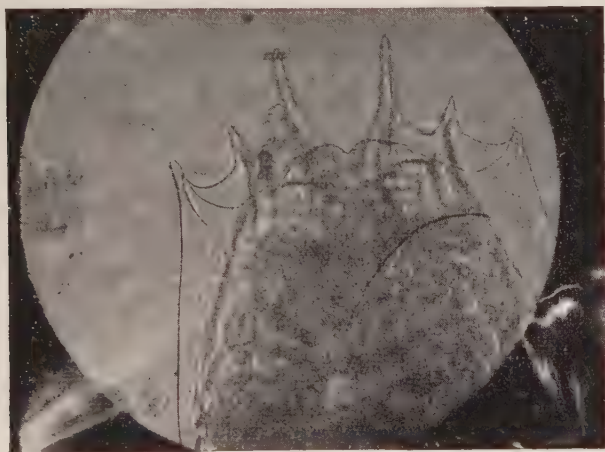

Abb. 8.

Abb. 9.

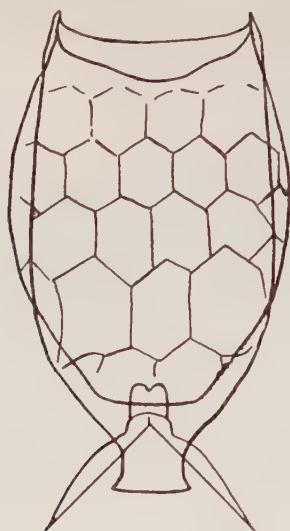ist also nicht nur beträchtlich kleiner als die Stammform, sondern auch als die var. africanus.

Abb. 10.

Lecane ichthyoura (ANDERSON- SHEPHARD). Exemplar mit gefeldertem Panzer

Lecane ichthyoura (Anderson-Shephard). (Abb. 10.)

Diese Art wurde schon mehrmals in Ungarn gefunden (vergl. GY. KERTÉSZ (4)), gilt aber als selten. In den Natronteichen war sie auch nicht häufig, kam aber mehrmals vor. Auffallenderweise war der Panzer unserer Exemplare deutlich in sechseckige Felder geteilt.

Körpermasse: Gesammtlänge 140 μ, grösste Breite 85 μ, Zehen 37—39 μ.

Lecane sinuosa n. sp. (Abb. 11.)

Panzer des kontrahierten Tieres elliptisch-rhomboidal, am Vorderende rund, hinten beinahe gerade abgeschnitten. Maximale Breite bei der Mitte des Panzers. Der Rückenpanzer überragt weit den Bauchpanzer und hat am Fussende zwei Pseudosegmente, das erste bei dem Ende des Bauchpanzers, das zweite bei dem vorletzten Fussglied. Diese sind durch deutliche Abstufung von einander getrennt. Die Seitenlinie des ersten Pseudosegmentes ist wellig, deutlich eingebuchtet. Das zweite Segment ist flach, Schüssel-förmig, endet fast geradlinig, nur ein wenig gerundet.

Der Bauchpanzer ist wesentlich kürzer und schmaler als der Rückenpanzer, verschmälert sich kaum gegen das Fussende wo es plötzlich, leicht gerundet abgeschnitten ist.

Die Kopföffnung ist ganz ungewöhnlich gestaltet: es ist ein kreis-

runder Ausschnitt am Bauchpanzer, an der betreffenden Stelle nur
etwas breiter als die halbe Panzerbreite. Der Bauchpanzer umgibt
sie nur bandförmig; sie scheint am vorderen Ende nicht geschlossen.
Die Kopföffnung wird so vorne von dem Rande des Rückenpanzers
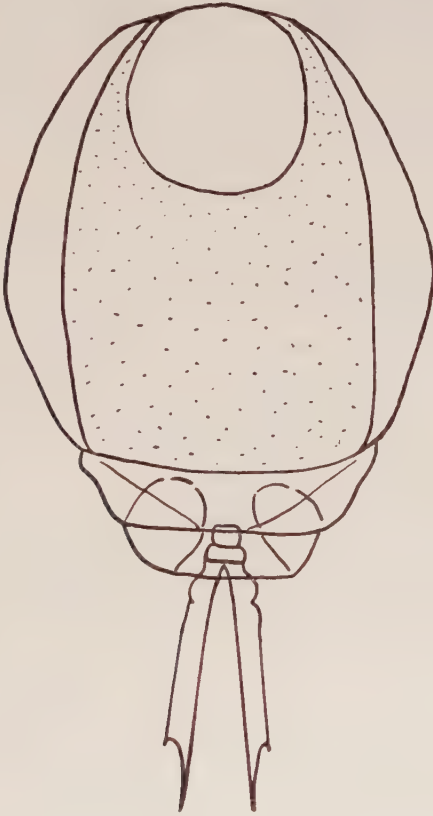begrenzt. Der Rückenpanzer ist glatt, der Bauchpanzer aber grob
gekörnt.

Abb. 11.
Lecane sinuosa n. sp.

Die zwei Pseudosegmente tragen von der Bauchseite gesehen zwei
schräg gestellte halbelliptische Linien, die beide Pseudesegmente
erfassen. Überdies laufen noch zwei fast gerade Linien oder Falten
von der äusseren Ecke des Bauchpanzers gegen den Fuss, und enden
an der Grenze des zweiten Pseudosegmentes.

Der Fuss ist klein, breit. Die Zehen sind mässig lang, oben ein we-
nig nach innen gekrümmt. An der äusseren Basis ist eine wellenartige
Verdickung, die mit einem scharfen Einschnitt in die Zehe übergeht.

359

Die Zehen tragen eine doppelte Spitze. Die äussere ist klein, spornartig und geht mit einer seichten Bucht in die Hauptspitze über, die ungefähr ein viertel der ganzen Zehe misst.

Die Art wurde Ende Mai in mehreren Natronteichen gefunden, war aber nicht häufig. Körpermasse: Länge der dorsalen Platte 128—132 μ, Breite der selben 93 μ, Länge der ventralen Platte 100—102 μ, Breite der selben 70 μ, maximale Dicke 70 μ, Durchmesser der Kopföffnung 44 μ, Zehe 57 μ.

LITERATUR

1. AHLSTRÖM, E. H. - 1940 - A revision of the Rotatorian genera Brachionus and Platyias; *Bull. Amer. Mus. Nat. Hist.* 77: 143.
2. BARTOŠ, E. - 1952 - Ceske druhy virnicki rodu Brachionus a Platyias kličem k určováni všech druhu obou rodu; *Časopis Nár. musea pris.* 169.
3. HUTCHINSON, G. E., PICKFORD, G. E., SCHUURMANN, J. F. M. - 1932 - A contribution to the hydrobiology of pans and other inland waters of South-Africa. *Arch. Hydrobiol.* 24: 1.
4. KERTÉSZ, G. - 1955 - Neuere Beiträge zur Systematik und Verbreitung von Lecane ichthyoura. *Zool. Anz.* 154: 245.
5. MAUCHA, R. - 1949 Einige Gedanken zur Frage des Nährstoffhaushaltes der Gewässer; *Hydrobiologia* I: 225.
6. MORRIS, C. B. - 1913 - Some notes on Rotifera not previously recorded as occurring in New-Zealand; *Trans. N. Z.Inst.* 45: 163.
7. NOGRADI, T. - 1956 - Limnologische Untersuchungen an Natrongewässer der ungarischen Tiefebene. *Hidrólogiai Közlöny (Hydrologische Zeitschrift, Budapest).* 36: 130.

Anschrift des Verfassers:
dr. Thomas Nógrádi
Budapest II. Lublói utca 5.
Ungarn.

An ecological study of the algae of the Saline River, Michigan

by

John L. Blum

Canisius College

TABLE OF CONTENTS

INTRODUCTION

Throughout the period of greatest activity of European workers on stream self-purification and indicator organisms (1900—1910), and the period of special interest in the benthic vegetation of streams

(1920—date), the algal vegetation of American streams has remained relatively unexplored. Following the classical work of KOFOID (1903, 1908) on the plankton of the Illinois River, no work even approximately comparable was undertaken on other rivers for many years. Reports on the phytoplankton of several American rivers have since appeared; these include the following rivers: the Potomac (PURDY 1916), the San Joaquin (ALLEN 1920), the Ohio (PURDY 1922), the Illinois (PURDY 1930), the Mississippi (REINHARD 1931), the Sangamon (EDDY 1932), the Hocking (ROACH 1932), the Huron (CHANDLER 1937), and others. The communities of algae in Florida spring streams has recently been studied (WHITFORD 1956). In general, knowledge of our stream algae lags well behind the relatively precise and abundant information which is at hand for European streams, particularly for those of Germany and Great Britain. Even in Europe, however, a general overall picture of seasonal changes and geographic changes in plankton or benthos has to date been wanting, due partly to the absence of sufficient observations as well as to the need for synthesis of those observations which have been published. While this is true even for unpolluted streams, it is doubly so for the very heterogeneous polluted ones.

ACKNOWLEDGMENTS

DESCRIPTION OF THE STREAM INVESTIGATED

This study was undertaken in the hope of throwing light upon certain subjects insufficiently known with reference to American streams, namely (1) the algal communities present, (2) the seasonal periodicity of the principal river algae, and (3) the differences existing between the benthic algal flora of clean-water and polluted portions of a stream.

The Saline River, located within Washtenaw and Monroe Counties in southeastern Michigan, was chosen for investigation. Its total length along its axis is 65.3 km, and the total surface area of its basin covers about 305 sq. km. It takes its source in small creeks which drain agricultural land in the southwestern portion of Washtenaw County about eighteen km southwest of Ann Arbor (Fig. 1). The course and flow of the river as a whole is in a southeasterly direction. After passing the small cities Saline and Milan it flows into the Raisin River near Dundee, and its waters are thence carried into Lake Erie close to the far western end of the latter. It should be emphasized that the name of the Saline is a misnomer: it is neither saline nor a river, having a small volume of flow of essentially fresh water.

At the time of this study (1951—53) the headwater region of the stream, a course of some 9.6 km, received no appreciable pollutants except for drainage from cropped soils, and it may be supposed that the stream above the city of Saline was essentially unpolluted. At Saline, the first source of pollution was from a constant-flow industrial outfall of considerable magnitude. The importance of this effluent to the life of the stream is due to its content of certain poisons lost in plating processes. For some distance, the stream received no other pollutants excepting, probably, minor amounts of seepage from the city dump, and it was thus possible to observe the effects of the industrial pollutants unmixed with large amounts of sewage. At a point about two hundred meters downstream from the industrial outfall was located a second major outfall which introduced raw sewage from the city itself. A determination of this sewage made October 7, 1952 showed a pH of 7.7, turbidity of 120, 3.60 mg per liter of inorganic phosphorus, no demonstrable nitrate nitrogen, but 21.5 mg per liter of total nitrogen. Beyond this point the river was highly polluted, and developed, at least in summer, a polysaprobic flora of *Sphaerotilus*, other bacteria, and filamentous fungi. Much further downstream it was possible to observe the effects on the algae of increasing dilution of the pollutants, as the organic particles settled out and underwent chemical change, and tributaries introduced clean water. Just above the city of Milan, a distance of about 14.4 km, the river had become approximately oligosaprobic once again,

in spite of certain intermediate outfalls of lesser importance. At Milan the river received further excessive amounts of domestic sewage and became heavily polluted for much or all of the remainder of its course. It was thus possible to observe, as one advanced downstream from the headwaters, (1) an unpolluted portion, (2) a polluted portion bearing industrial wastes, (3) a polluted portion bearing both domestic sewage and industrial wastes, (4) a zone of recovery which gradually replaced zone (3), and (5) a highly polluted portion.

The principal tributaries of the Saline have been assigned numbers in Figure 1. Certain of them, notably Tributary 15, have their origin in permanent springs with a steady flow of water, which ensures the presence of water in the river itself the year around. The majority of the tributaries originate in part from surface runoff, in part from seepage springs, and, in addition, are further augmented in their lower courses from the same two sources. The principal tributaries are more or less permanent creeks with a relatively small volume of flow. They drain land whose use was largely agricultural, with a large percentage of the land in pasture and another considerable portion fallow or abandoned; but portions were wooded, other small portions were urban or suburban, and others were industrial or recreational in use. In many places the flood plain of the river is covered by thickets which render portions of the river difficult of access.

The major portion of the upper course of the river lies upon the abandoned bed of a ponded section of the glacial Huron River. Just west of the city of Saline, the Saline River turns to the south (Fig. 1) and passes through a narrow channel cut across the Defiance Moraine. This channel was cut by the Huron River in later glacial times when the Huron emptied for a brief period into Lake Maumee at Saline. Later the Huron was diverted to its present channel north of the Saline basin, whereupon the formerly ponded area west of Saline began to drain through the abandoned channel of the Huron across the Defiance Moraine. The drainage system thus established formed the Saline River, which therefore had at its inception an extensive headwater system already developed (BAY 1938).

Drift in the Ann Arbor area, deposited in Wisconsin times as well as in earlier glaciations, is as much as four hundred feet thick (RUSSELL & LEVERETT 1908). The erosive removal of soil and smaller stony particles has resulted in massive accumulations of polished rocks in the valley of the Saline River and on the floor of its numerous riffles (shallows), especially where the river crosses the Defiance Moraine. Many of the pools, the portions of the river between adjacent riffles, manifest in this area similarly rocky bottoms which commonly are thinly covered over with sediments.

Once the river leaves the region of the Defiance Moraine and enters

the bed of glacial Lake Maumee, its character changes: it meanders more frequently; few riffles are found in the remainder of its course; and what riffles are found are less differentiated — the stony material which underlies their floors and their crests consists of pebbly detritus and of much smaller stones than those found nearly everywhere above the third Maumee beach. The bed of this lower portion of the river is composed largely of a deep deposit of silt and organic materials.

Two impoundments of the river exist, one at Saline, the other at Milan, and each with a surface area of about 8 hectares. These impoundments will henceforth be referred to as „Saline Pond" and „Milan Pond" respectively. A millrace at Milan Pond diverted a considerable flow of water, whereas a similar millrace at Saline was inactive throughout the period of this study.

The numbered stations on the stream (Fig. 1) which were chosen for the most intensive study may be characterized as follows:

5. Unpolluted riffle just above the bridge on the Saline-Manchester road, and just below the mouth of Tributary 11. This is a headwater station with steady flow of water the year around, about 45% shaded in summer.

8. Unpolluted riffle about 200 m. downstream from the dam retaining Saline Pond. This riffle shows certain temperature and other influences from the pond. It was about 35% shaded in summer.

10. Unpolluted riffle about 100 m. downstream from Station 8. It It was about 35% shaded in summer.

12. Unpolluted riffle in woods, about 200 m. upstream from the Macon Road bridge. It was about 95% shaded in summer.

14. Polluted riffle at Saline dump, just below the Macon road bridge. The stream at this point carried industrial wastes and was about 65% shaded in summer.

15. Heavily polluted riffle just below the sewage outlet for the city of Saline, about 100 m. downstream from Station 14 and about 65% shaded in summer.

18. Heavily polluted riffle about 100 m. downstream from Station 15 and about 50% shaded in summer.

The upstream stations 1—13 were oligosaprobic and are referred to in this paper as the „headwaters stations". Stations 15—20 and 34—37 may be regarded as belonging to the polysaprobic zone of KOLKWITZ & MARSSON (1908). Stations 21—24 correspond to the α-mesosaprobic, and Stations 25—32 (principal zone of recovery), as well as Station 14, to the β-mesosaprobic zone.

In general, standard methods of collection, preservation, and che-
mical analysis were used.

Light. — Measurements of incident light were made with a No.
594 Weston waterproof cell attached by water-tight seal at the end of
a five-foot pipe which houses the leads from the cell. This apparatus,
when used at arm's length, permitted readings on the river bottom at
a horizontal distance of about 1.8 m. from the operator and at depths
up to nearly 1.2 m., which was sufficient for the present study. The
leads from the cell were connected to micro- and milliammeters of
suitable range.

Turbidity. — A turbidimeter was not readily accessible. Turbidity
was determined roughly in the laboratory with a Klett-Summerson
colorimeter utilizing a blue filter. This instrument was calibrated
against a Hellige turbidimeter.

Rate of current was measured by a modified Pitot tube utilizing a
manometer (WELCH 1948, p. 144). This instrument was calibrated
against a Leupold and Stevens current meter.

Hydrogen-ion concentration was determined regularly with a Beck-
man pH meter in the laboratory, within four to twelve hours after
collection.

Dissolved oxygen, carbonate, bicarbonate, salinity, and *hexavalent
chromium* were determined by standard methods[1]. For all determin-
ations of dissolved oxygen at points on the river above the industrial
outfall, the Winkler method (unmodified) was used, and titrations
were followed to completion in the field. For determination of dissol-
ved oxygen from all points on the river below the industrial outfall,
the Rideal-Stewart modification of the Winkler method was em-
ployed; the first steps of this analysis were accomplished in the field,
and the titration was completed in the laboratory.

Unless otherwise specified, all water samples, including those for
dissolved oxygen, were taken from undisturbed surface water accor-
ding to methods recommended for the respective tests.

Nutrients. — Samplings and tests for essential nutrients were made
from a series of „key" stations at approximately ten-day intervals
throughout a fourteen-month period. These 5—7 stations regarded
as the most important were all included in the samples taken on virtu-
ally every such day, but the number and identity of other stations
tested on any one sampling day was variable. With this flexible proce-
dure, it was found possible to keep more satisfactory account of the

---

[1] *Vide* WELCH 1948 and Standard methods for the examination of water
and sewage (Edit. J. F. Norton 1946).

entire river, and it is believed that much was learned, and that many facts which would otherwise have been missed were brought out by the occasional samplings from new and relatively unvisited stations on the stream.

Tests for inorganic phosphate were made by the method of Fiske & Subbarow (1929) based on the reduction of phosphomolybdic acid to blue molybdous compounds. Tests for nitrate were made by the Rietz modification of the Feigl method, which depends upon the oxidation of the colorless diphenyl amine to form a blue dye in the presence of nitrates and in an acid medium (Feigl 1937). Total nitrogen was determined colorimetrically by reaction with Nessler's reagent after digestion according to the method of Koch & McMeekin (1924).

Biological — Qualitative. — Observations of the stream and collections of algae were made regularly at approximately ten-day intervals throughout a period of about 14 months. Prior to that time the stream had been under observation at approximately monthly intervals for six additional months. Algal species present in significant numbers were determined. Species, especially microscopic ones, represented by only a few observed specimens were in general ignored, unless actually attached by some means which showed conclusively that they were not merely adventives in the locality. Specimens of algae have been filed in the herbaria of Professor William Randolph Taylor, of the University of Michigan, and of the author.

Qualitative collections spaced about ten days apart were commonly made at Stations 5, 8, 12, 13, 14, 17, 18, 25, and 28. Stations 9, 10, and 15 were visited at approximately three-week intervals. In addition numerous other established stations were visited and sampled at irregular intervals throughout the year, and portions of the stream above and below Saline and Milan were investigated at different times on foot. It is felt that a general understanding of the stream vegetation would have been seriously curtailed if such surveys afoot over considerable horizontal distances had not been made, and if the study had been confined to the observation from month to month of rather rigidly delimited stations.

In general and with time it became possible to recognize in the field nearly all the important species of algae and their colonies, except for absolutely microscopic and planktonic forms. For purposes of field work, a macroscopically varied algal vegetation with numerous distinctive species, as in the Saline River, is a great advantage.

Biological — Quantitative. — Methods used in the quantitative measurement of algal growth included (1) transects of the stream at monthly intervals, (2) dry weight determinations of the most important algae, (3) placing of sterile rocks within the stream and observa-

tion of subsequent colonization on them, and (4) phytoplankton counts.

The „transect" method which was evolved after some trial and error is a modification combining some of the features of both the transect method and the list quadrat, and is especially useful for ecological work in streams. A rope marked off into decimeter and meter units is stretched across the stream at a riffle and as close to the water as possible. Presence is recorded in alternate decimeters of all algal species an individual or colony of which is crossed by the rope. If a tuft or colony of a given species was present in a given decimeter of the vertical plane through which the rope passed, that species was, therefore, counted as present and no further record was made of its importance in that particular decimeter. The importance of a species was thus determined by the relative number of decimeters within which that species was present. Alternate rather than consecutive decimeters were recorded in order to avoid the effect of grouping. Frequency was obtained for each species present by determining the relative percentage of the total decimeters in which it was found in relation to the total number of decimeters whose composition was recorded. Usually two or more such transects were made at each such visit to a station, until a total of 50—100 decimeters had been recorded for that station on that day. These transects were all oriented at approximately right angles to the direction of water movement, and all were located with the intention of providing a typical cross section of the riffle. This method is not applicable to pools, and is workable only with difficulty even on riffles when the water is 20 cm. or more in depth and when turbidity is high.

In the early portion of the work records were made of the complete transect, from bank to bank. Portions of the stream near the bank, differing in depth or in rate of flow or in both these factors from water across the more central portion of the stream, were recorded separately from midstream portions. As work progressed, it was found that the edges of the stream, atypical as they were, involved so many ecological variables that statistical observation of the changes there would be a study in itself. In order to obtain more significant and more comprehensible data from the typical portions, quantitative records on the edges of the stream were discontinued: only those portions of the transect passing through apparently typical parts of the stream were considered. Qualitative observations of the edges of the stream were, of course, continued as before. The delimitation of „typical" portions of the transect was based upon near-average conditions prevailing there. A „typical" portion is essentially like the greater part of the riffle as regards average depth, apparent total incident light per day, the nature of the bottom, current rate, and composition of the water.

368

All visible species are reduced by this method to the same category, regardless of the level within the stream at which the species is found. Filaments of large algae such as *Stigeoclonium* or *Cladophora* recorded on the transect are likely to be attached at some point upstream but to float free within the water current at a vertical distance of some centimeters above other benthic forms which lie in the plane of the transect. Below the larger algae, the rocky bottom of the riffle may be covered over with an appressed crust of microscopic algae (Fig. 3) which are nevertheless visible as a colony. Above this hard, part mineral, part organic crust may be a layer of diatoms or a mat of blue-green algae which cover over and completely conceal the crustose forms below. After some experience it is generally possible to recognize the presence or absence of at least certain crustose forms even when they are covered over by a continuous layer of another species. Tabulation of forms present upon a given transect necessitates, therefore, the observation of species present at these different levels within the stream.

In practice, it was deemed unnecessary to record the presence or absence of certain of the crustose communities which remained present in apparently unchanged amount throughout the year and showed, in such quantitative determinations as were made of them, no significant seasonal variation. The forms recorded as present on a given transect were limited, therefore, to a series of conspicuous and important species or communities, certain or all of which fluctuated widely in frequency from season to season. Species forming colonies so small as to be inconspicuous to the eye, and non-colonial microscopic species were not recorded, along with the principal crustose sforms, whose seasonal variation, if indeed they have any, is not measurable by the present method.

Certain of the diatoms of streams form colonies which are easily distinguishable macroscopically. These were recorded by species on the transects. Certain other benthic, non-calcified diatoms grow in wide-spreading layers on the surface of submerged silt banks, and others will be found in fairly cohesive layers on rocks and on bottom gravel, even in areas of swift water. In polluted portions of the Saline River, such growths are likely to be limited to only one or two species, whereas in the non-polluted headwater portions of the stream a mixture of many diatom species is to be expected. In transect records the presence of such a ,,diatom layer'' was generally recorded as if it were a single species, and its composition was subsequently determined in the laboratory from samples taken at representative places on the transect.

It should be noted that even the colonies of such diatom species as are macroscopically recognizable are likely to contain a number of

other diatom species growing attached to or adherent in some way to the species which is principally responsible for the formation of the colony. Sometimes this is true to such an extent that observation with the microscope reveals a population of the epiphyte or cohabitant almost as large as that of the host or dominant species. In the ecological method here employed (transect), such species of secondary rank and the part they play in the formation of the entire diatomaceous ensemble are, of necessity, ignored.

Dry weight. — In the determination of dry weight of plants of certain algal species within the stream, certain peculiar difficulties are encountered: (1) Adequate sampling of the vegetation by the quadrat method is difficult or impossible without employing relatively large-area quadrats; (2) Denudation of large-area quadrats would be expected to have severe repercussions on the stream for many months thereafter — this might not necessarily be the case for a larger stream; (3) The delimitation of a given area of the bottom and the removal of all organisms from that area exhibits certain drawbacks when applied to those freshwater algae which form tufts or streamers extending downstream from their point of attachment. No matter which of the usual methods is employed, removal of such algae from the quadrat under consideration necessitates the severance of all algal filaments from their portions which lie upstream or downstream from, and lateral to, the sampling area. No deleterious effect results on the upstream side of such a quadrat, but severance of algal streamers from their downstream portions may set free large masses of algae which had their attachment somewhere within or upstream from the sampling area. For *Cladophora* species which have streamers up to two meters in length in certain seasons, such changes may be considerable.

Because of these difficulties, a different method of sampling was developed. It consists in the removal of a given quantity of bottom material with all attached vegetation, no matter what position in the stream the attached vegetation occupies. Overlying vegetation attached upstream remains essentially undisturbed; all algae remain, in fact, undisturbed, except those complete plants which are removed from the stream. In practice, twenty rocks are removed at random from the riffle bed by means of a grapple. The rocks are laid in a row in arbitrary order upon the bank, and alternate ones to a total of ten are then removed and placed on the pan of a spring scales, or in a pail, for weighing. If the ten rocks together weigh twelve pounds ($\pm$ 0.5 lb.), they are used as the sample and the other ten are returned to the stream. If the ten rocks when weighed amount to more or less than twelve pounds, one or more smaller (or larger) rocks chosen from the ten still remaining on the bank are substituted for an

370

equal number of those being weighed, until ten rocks have been found which weigh twelve pounds ($\pm$ 0.5 lb.). Their algal vegetation is removed and placed in a collecting bottle. These ten rocks are then returned to the stream at a point chosen for this purpose, which is henceforth avoided when making ecological observations. The remaining ten rocks are also returned to the stream.

The ten rocks thus used in sampling the stream are assumed to represent a typical standard portion of the stream bottom, to expose a standard surface to the overlying water layer, and to be inhabited by a standard population of algae. In the present study, limitation of time prevented the taking of monthly samples of this type for more than the most important and conspicuous filamentous forms. The species chosen for these records were *Cladophora glomerata* (L.) Kütz., *Batrachospermum boryanum* Sirod., *Stigeoclonium tenue* Kütz., and the bacterium *Sphaerotilus natans* Kütz. This method is most serviceable for the large filamentous algae; it would be applicable to the crustose forms, and with greater difficulty to certain of the diatoms.

After return to the laboratory, the algal material is removed from the collecting bottles and divided for washing into portions of suitable size. It is then washed portion by portion on a 20 cm. square of window screening which is supported on a glass cylinder with open ends. In this washing, which must be done manually, a jet of tap water of considerable force is directed down onto the algae, and is continued for each portion of the algal material until the wash water in the cylinder below is essentially free of turbidity. *Stigeoclonium* and *Sphaerotilus* are easily washed in this way. *Cladophora* species must be separated out and constantly untangled as they are being washed, or no amount of washing will remove all of the attached sand and grit. After thoroughly cleaning each portion, many small grains of gravel remain nevertheless adherent to the *Cladophora* — these must be removed individually with fingers or forceps. When the algal material is free from mineral particles, it is placed upon a square of powder paper of known dry weight, dried to constant weight in a drying oven, and its weight determined.

The principal sources of error in this method may be summarized as follows:
1. The error resulting from the fact that only rocks within a certain size range are included in the collection. Boulders and other rocks above a certain size are too heavy to be removed from the stream by conventional methods; and rocks which are too small to be retained by the grapple are obviously not included in the sample.
2. The error resulting from the impossibility of removing by this method all algal filaments from a rock. The relative smoothness or

roughness of the rock surface is a factor contributing to this error.

3. The breakage and removal by the current (largely unknown to the operator) of small or large portions of algae while the rock is being removed from the stream bed. This is very common and almost unavoidable with *Stigeoclonium tenue*, *Sphaerotilus*, and almost any alga with a heavy, gelatinous thallus.

4. The inclusion of numerous caddis fly webs in certain types of vegetation, particularly *Cladophora*.

5. The inclusion of a few small mineral particles in masses of *Cladophora*, unavoidable unless each grain is removed by hand.

6. The greater wet weight of very large masses of algae, and the resulting slight reduction in weight (and hence in exposed surface) of the ten rocks selected for sampling.

7. The unavoidable inclusion with the benthic filamentous vegetation, of fragments of similar (or other) algae caught in the algal filaments. The most important fraction of this error is the numerous filaments of dead or living *Cladophora* caught or anchored in those caddis fly nets which are incorporated into the benthic vegetation. Frequently the adventive algae are branching systems which much resemble young plants growing *in situ* and cannot be readily distinguished from them without studying each plant individually.

8. Epiphytic organisms — a particularly important source of error in *Cladophora* determinations in fall and winter. Many of these epiphytes deposit carbonates outside their thalli, which can become a continuous crust about the filaments of the host and in this way likewise increase its apparent dry weight.

9. The breakage and disappearance in the washing process of many algal filaments.

Many of these sources of error, for example numbers 5 and 9, tend to balance each other to a certain extent. Nearly all are such as could by some means be avoided in whole or in part if an unlimited amount of time were available. Future workers who become interested in such problems regarding benthic river algae will find that methods comparable in precision with those now applied to a study of fresh water and marine plankton can be worked out readily enough, but it is likely that such methods will be distinctly more time-consuming and will demand even greater care and patience on the part of the operator than do the standard plankton methods of the present time.

Colonization on Sterilized Rocks. — For a study of colonization and succession, large, glacially-polished rocks weighing 3—5 kilograms such as occur commonly in local drift (and on the stream bottom), were collected from a morainal deposit and sterilized by

heating dry in an electric oven at a temperature of 200° C. for five hours. Each rock was labeled with a conspicuous number in black enamel and was placed, with the number down, at a given locality in the stream. Precise note is taken of the date and the exact spot where the rock is placed. Rocks of this weight are not often displaced, even in fast currents, and although trouble was occasionally experienced in recovering certain rocks, none were permanently lost. Finding the rocks on a subsequent date is facilitated, and their removal by the current rendered more unlikely, of they are arranged in a straight row parallel to the direction of flow, on the stream bed.

Colonization and succession is soon apparent on such rocks even when viewed through the layer of moving water. For careful observation of their vegetation, they must be removed from the water momentarily. Samples of the vegetation can be collected at this time for study in the laboratory, but it is necessary to make careful note of the portion of the surface from which the sample was taken so that this disturbed area will not be mistaken for typical vegetation on the next inspection of the rock. As soon as observation has been completed and samples, if any, taken, the rock is returned to its position in the stream. A series of such rocks, placed in the stream on successive dates and examined at intervals of ten days thereafter, provides information as to the times and conditions of reproduction of many algae in the river and convincing evidence of algal colonization on the river bed.

Plankton counts. — For determination of net phytoplankton, the method of Verduin (1951) was followed.

CLIMATOLOGICAL DATA

The summer and fall of 1952 was a period of unusually low rainfall in southeastern Michigan. Summer precipitation recorded for this period at the Willow Run airport, at a distance of about 22 km. from both Saline and Milan, was only about one half that of the same period of 1951. Because of low rainfall, the water level in the river remained relatively low, and almost unchanged, throughout most of the summer and fall of 1952, with short and very infrequent periods of higher water occurring at intervals (Fig. 5). A short period of unusually high water occurred on March 5 or 6, 1953, following heavy rains (47.6 mm.) on March 4. High water marks found on March 7 were about 0.6 meters above the usual level of the water at Station 5, and about 1.0 meters above the usual water level at Station 12.

The year 1952 was likewise unusually warm, with temperatures of 90° F. (32° C.) recorded on thirty-three days, as compared with the

usual expectancy of about thirteen such days. From one standpoint, it was unfortunate that one of the years in which this study was made should not have been a typical one in this respect. From another and at least equally important standpoint, it was of signal advantage to be able to observe visually the riffle beds at nearly all visits throughout 1952. Certain types of ecological work performed would have been hindered if not completely prevented by water above the level maintained in the portions of the stream which were worked most intensely.

THE SALINE RIVER AS AN ALGAL HABITAT

Temperature. — Temperature changes of the river water followed those of the surrounding air (Fig. 4) but were less extreme and less rapid than those of the air. Temperatures of the river above the pond in Saline appeared to be more readily influenced by changes in air temperature than at stations immediately below the pond. Records based upon simultaneous readings at a series of points are unfortunately not available. However, there seems little doubt from data obtained October 16, 1952, a day following a sudden drop in temperature, that the pond, at least in seasons of great thermal change, acts as a thermal stabilizer for portions of the stream immediately downstream from it. Readings made on this date showed an increase in water temperature at Station 5 (above the pond) of nearly six degrees from morning to afternoon. Surface waters of the pond itself showed an increase at Station 7 of only 1.5 degrees in the same approximate period. Station 8, just below the pond, had an increase of 1.7 degrees, and Station 28, at 3.2 km. below the pond, an increase of 2.6 degrees.

Light. — The amount of light reaching algae growing near the surface of the Saline River does not appear to differ greatly in amount from that reaching low herbs which grow on adjacent banks. An alga growing in an unshaded position must therefore be able to withstand full sunlight almost unreduced in amount, but its photosynthetic system in return enjoys the advantages of copious radiant energy. This energy reaches a maximum at about 12 : 30 P. M. each day in the Ann Arbor region and of course varies in duration and intensity with the changing seasons. Light readings made under water in algal communities of the stream suggested that no one position in the stream remained constantly in the sun and probably there are very few which remained constantly shaded. Peculiarities of the stream's course, the character of the bottom, and particularly the ever-present bank vegetation militate against such constancy of incident light. Hence, the amount of radiant energy reaching a given river alga in fair weather can almost never, even on cloudless days, be expected

to follow the curves for total light but instead, for a given depth, must range between the curve for a sunny position and that for a shaded position.

In winter, the leafless branches of overhanging trees have little effect in reducing diffuse light from a cloudless sky, as was shown in data obtained in February, 1952. The trunks and large branches of trees located 20—50 meters from the stream on its southern side, however, can effectively shield the stream from the direct rays of the sun. Such trees, provided the sun can clear them, may have no effect on river algae in summer even though they are in full leaf, whereas in winter they sharply reduce the incident light reaching the stream.

Variation in total radiation with depth is probably insufficient to limit plant growth in most small streams. Depth of riffles is not sufficient to reduce surface light to a significant degree, and in the Saline even pools are seldom deeper than 1.5 meters. At depths measured in Station 17, total light at sunny portions of the bottom was always greater than diffuse light at the shaded surface points. Sufficient light reached the stream bed here to permit the growth of *Navicula atomus* (Näg.) Grun. apparently at all depths. With increase in stream depth, light may be expected to become a limiting factor in plant growth, but it seems likely that in streams of low turbidity the factor of depth carries much less importance than in any lake of ordinary depth.

Turbidity. — In the Saline River turbidity did not vary appreciably from source to mouth, with depth, or with the seasons. At the points of entry of sewage from the cities of Saline and Milan a slight increase in turbidity was noted. This was dispersed, presumably by settling out and chemical action, within the distance of a few hundred yards. No seasonal variation in turbidity was observed. Following heavy rains, suspended matter in the river rose sharply in amount and remained relatively high for a period of about twenty-four hours, when a rapid return to the usual low turbidity could be observed. A similar increase in turbidity occurred with the melting of large quantities of snow and ice in winter and spring. The usual range of turbidity, recorded in approximately 90% of the samples, was from 6 to 20 parts per million. A maximum turbidity of 212 p.p.m. occurring after rains was recorded at Station 8 on November 17, 1952. A minimum turbidity of 4 p.p.m. was recorded on several occasions.

Current. — In the Saline River average current velocity on riffles was from 0.30—0.90 meters per second, with a maximum rate at low water of 1.35 meters per second recorded at Station 8. In the area immediately downstream from large rocks, areas of no movement as well as of upstream water movements were clearly evident. Measurements of current made in the vicinity of rocks anchored at a depth of

4—5 cm. in the stream bottom showed that the zone of influence of the rock on the current enlarged downstream from the rock in such a way that at a distance of 20—25 centimeters downstream the velocity of even the surface water was greatly reduced. This protected area of slight water movement is the habitat of massive filamentous microphytes such as *Cladophora glomerata*, *Stigeoclonium tenue*, and *Sphaerotilus natans*, and for algal growth seems to be one of the most favored situations in a stream. Individuals of none of these three massive thallophytes are confined to such a situation, however. Good local growth of all of these organisms can be observed in almost still water neighboring regions of rapid water. The actual amplitude in water velocity in the measurable layer closest to masses of these plants is very near the amplitude of all determinations within the stream, namely, from 0.0 to 1.35 meters per second, with optimum growth of *Stigeoclonium tenue* occurring at velocities of 0.35—0.85 meters per second.

The importance of currents and eddies in algal distribution has been observed repeatedly in virtually all parts of the stream. The benthic and semi-benthic algae of pools are particularly dependent on eddies for their vegetative dispersal. The shoal area „A" which is shown diagramatically in Figure 2 is typically the inside curve of a meander. It is shallow at its edge and slopes off gradually so that it exposes a wide strip of slight depth to the sun. At the same time it is usually an area of slow counter-current within which the river has dropped abundant silty sediments. Numerous algae make capital of this coincidence of a highly illuminated photosynthetic zone and a zone of abundant nutrients. It is, furthermore, a region well adapted to the successful dispersal of the algae, for although measurable current at the bottom (at a depth of 10—20 centimeters) is nil and thus permits the growth and reproduction of unattached forms, the surface water is in slow circular motion. The mechanism is as follows: (1) At times of rapid photosynthesis, individual masses of the algal filaments are detached and buoyed upwards by the trapped oxygen bubbles; (2) once the algal mass has quitted the floor of such a shoal, it is carried slowly along in the eddying surface water; (3) after moving for some time in this circular manner, the algal mass may eventually be picked up by the current in the main stream, which removes it definitively from the shoal; (4) travelling downstream, it disseminates live filaments along the way. The progress of these filaments is arrested on obstructions or on new shoal areas, which in this way are themselves colonized. The clearest examples of this manner of dispersal were observed at Stations 7—13 for *Oscillatoria tenuis* Ag. and at Stations 15—20 for *Spirogyra spp.* during the summer of 1952. The elevation of algal masses by entrapped bubbles can be observed from about noon until 2—3 P. M. on sunny days in

July, and the movement downstream of thousands of these floating masses, which have their origin on the floor of shoals or of pools, can be observed throughout the entire afternoon.

Hydrogen-ion concentration. — It has been shown by BRUJEWICZ (1931) and others that a definite diurnal variation in pH can occur in streams. Hence, pH data taken at various times of day and at various stations, such as the data recorded for the Saline, cannot be regarded as having more than local and temporary significance. However, it seemed clear that no seasonal variation in pH occurred in the Saline, and that little if any significant change occurred from source to mouth. The sewage effluents discharged from Saline and Milan had a pH of about 7.5, slightly below that of the river, and a correspondingly slight depression of the pH of the river water could usually be observed for a short distance below these effluents. The river was well buffered, and little variation from the usual pH range of 7.8— 8.5 was observed. No consistent difference between the pH of polluted and of clean parts of the river was observed, either in winter or in summer, in spite of the presence of a rich winter vegetation of algae in unpolluted portions of the stream, and its absence (in winter) in polluted portions generally.

Dissolved oxygen. — It is well known that dissolved oxygen is greatly reduced in a stream below sewage outfalls, due largely to the metabolism of abundant aerobic bacteria. (BUTCHER 1940, 1949 and others). In the Saline River, such reduction is evident in the region from Station 14 to Station 28. Except for this area, dissolved oxygen is abundant throughout the upper part of the stream. Rapid flow, the presence of numerous riffles, and relatively slight depth all contribute to the generally favorable oxygen content.

No significant variation of dissolved oxygen with depth was found in the Saline River. Presumably the stream is shallow enough in its entire course above Milan, so that no measurable dissolved oxygen gradient ever exists between the upper and lower strata of water.

Dissolved oxygen varied markedly with time of day. Determinations made in water of the riffle at Station 8 in August, 1952, and in water of the pool at Station 17 in September, 1952, showed a slight but unmistakable decline in dissolved oxygen during the night. The diurnal change in dissolved oxygen has already been recorded by BUTCHER, PENTELOW & WOODLEY (1930), BRUJEWICZ (1931) and others.

Bicarbonate. — Saline River water was found to contain large quantities of bicarbonate. Actual amounts varied from 172.0 parts per million, recorded September 15, 1952 at Station 12, to 287.0 p.p. m., recorded the same date at Station 5. In general, Station 5 showed a higher concentration of bicarbonate than other stations farther

downstream, but no other consistent change with distance along the course of the stream was observed. The industrial effluent at Saline always showed exceptionally large amounts of bicarbonate which varied from 273.0 p.p.m. (July 21, 1952) to 335.5 (February 25, 1953).

Chlorinity and Salinity. — Chlorinity and salinity were determined at a series of stations on December 16, 1952. Values for both ions were found to be relatively high (chlorinity 0.125 p.p.m., salinity 0.250 p.p.m.) in the effluent from the factory at Saline. But all readings in the river itself were below 0.07 p.p.m. for both determinations.

According to local residents, the Saline River owes its name to a salt spring formerly located in the river valley near Saline. The low values obtained for chlorinity and salinity throughout the course of the stream, however, would seem to demonstrate that such a spring, if it exists at all, is of little importance to the chemical make-up of the river.

Inorganic phosphate. — Inorganic phosphates were uniformly low in unpolluted portions of the Saline River. With the entry of the effluents from the factory and from the city of Saline, they increased approximately tenfold in the stream and remained high for a distance of 200—300 meters. From about Station 20 to about Station 28, a steady decline in inorganic phosphates was apparent. Below Station 28, a slight secondary increase in phosphates due to the hospital outfall at Station 29 was evident, but they remained relatively low at Station 30 between Mooreville and Milan, and at Station 32 above the Milan outfall. Below Milan a sharp increase in inorganic phosphates was found, due again to massive accessions of sewage.

In addition to marked differences in the amounts of inorganic phosphate within the stream at any given time, clear seasonal variation was evident (Fig. 6). Much larger amounts of phosphate were recorded in polluted portions of the stream throughout the summer period than in the winter. A similar but less striking difference was evident in unpolluted portions of the river. Throughout December, 1952 and January, 1953 inorganic phosphates remained low in amount in all observed parts of the river.

Nitrate. — In the headwaters area, certain streams quite consistently showed 1—3 parts per million of nitrate while others as consistently showed much less or none. Station 5, for example, rarely had as much as 1 part per million, whereas Tributary 11, entering just above this station, regularly had 2—3 p.p.m., as did Stations 8—12 (Fig. 7). Although water lost from the factory effluent contained small amounts of nitrate, the nitrate-free sewage entering between Stations 14 and 15 was largely a diluent of nitrate-rich water already in the river, and

378

Stations 15—18 were often lower in nitrates than were the stations upstream. With the progressive destruction of organic compounds and the oxidation of ammonium and nitrites, nitrates slowly increased in quantity in the lower course of the river, and at Station 32 just above Milan reached a high point of 3—5 p.p.m. which was maintained rather consistently throughout the summer.

Late summer was, in general, a period of low nitrate content in at least the upper and middle portions of the river (Stations 5—18). In November, following the disappearance from the river of nearly all the algal communities of summer and fall, a distinct rise in nitrates in these headwater stations was evident, and throughout the winter and early spring the concentration maintained in the unpolluted stations was often higher than in the polysaprobic stations (Fig. 7).

Chromium. — Tests for hexavalent chromium made at several points on July 25, 1953 showed no demonstrable chromium above the industrial outfall at Saline, 17.0 mg. per liter at Station 18, and steadily decreasing amounts below this point (Station 25, 12.5 mg.; Station 28, 12.0 mg.; Station 38, 4.0 mg.).

Animals. — The abundant and diversified animal life inhabiting the upper reaches of the Saline River disappeared almost entirely below Saline, and was replaced for much of the river's course by tubificids, numerous flagellates, and a few other organisms characteristic of polluted water.

Observations of animal life were more detailed at Station 8 than elsewhere. On this riffle *Cambarus*, *Dugesia*, and larvae of Trichoptera, Ephemeroptera, and Plecoptera were present at all times of the year. In late winter, spring, and summer larvae of *Simulium* were common. At Station 12, which was heavily shaded in summer, there developed in August and September several conspicuous colonies of green sponges. No other invertebrates of any size were commonly observed in the stream, but a considerable fauna of small fish attracted anglers throughout the summer months.

Of these organisms, the most significant with respect to algal life are probably the caddis fly larvae (Trichoptera). These small creatures construct galleries (Fig. 3) in the crustose growths of *Schizothrix* and *Phormidium* which are described below. It seems probable that the larvae ingest large quantities of this semistony layer in which they spend their larval life. In addition to the influence on algae consequent upon the erosion of this algal layer, the larvae incorporate fragments of *Cladophora* and other filamentous algae into their webs, and the exposed nets which they construct trap large numbers of *Oscillatoria* filaments in June and July. The algal filaments thus trapped frequently can be seen to reproduce and to form colonies *in situ*; hence, the caddis fly web may serve as a focus for secondary dispersal

of the alga. In late September, 1952, the nets of millions of these caddis flies formed a virtual floor to the riffles at Stations 8, 10, and 12, and occupied all exposed faces without exception of all stones which were surrounded by moving water. By mid-October, the great majority of these had disappeared from the stream, and in winter such caddis fly webs as remained were largely hidden by the abundant colonies of the winter diatoms. Caddis fly larvae were common in the stream throughout the year, but the massive riffle populations were in evidence only in late summer.

Plants. — Among the numerous ways in which other plants influence the algae of the river may be mentioned the following:

Shading. — Shading by bank vegetation has been discussed above. Shading by aquatic plants is of little importance in the Saline River, for only *Anacharis canadensis* (Michx.) Planchon grows in sufficient quantity to bring about reduction of light over large areas of the stream bottom, and *Anacharis* was not abundant in the river at any observed point below Station 6. Certain pools in the headwaters portion of the stream above Station 13 are characterized by meagre summer growths of various aquatic phanerogams, including especially *Heteranthera dubia* (Jacq.) MacM., *Wolffia punctata* Griseb., *Spirodela polyrhiza* (L.) Schlied., and a narrow-leaved species of *Potamogeton* which was never found in fruit. Probably none of these has more than local influence on the stream environment. At certain riffles, notably Station 12, aquatic mosses (*Fontinalis* sp. and *Fissidens grandifrons* Brid.) are common.

The shading of crustose or appressed algae on riffles by *Cladophora* and other large filamentous algae was very considerable at certain seasons. *Cladophora glomerata* grew in extremely dense skeins in late spring. Light determinations made with the light meter held directly below certain of these skeins and pointing vertically upwards frequently gave readings of 0.0 foot-candles at midday. Certain others of such skeins gave readings, according to their size and density, intermediate between zero and the quantity of incident light at comparable depths outside the algal community. Inasmuch as these algal masses move constantly back and forth in response to shifting currents, it is unlikely that any one point on the stream bottom is in permanent shade because of them. Nevertheless, many parts of the riffle unquestionably receive greatly reduced light because of these large algae.

Epiphytism. — Many benthic algae of streams are epiphytes on other algae or on higher aquatic plants. Because of the relative scarcity of phanerogams in the stream, and because of the absence of conspicuous algal growths on them, the diatoms epiphytic on or supported by these plants were not given careful study. The large river

algae, however, particularly *Cladophora glomerata* and *Oedogonium* spp. were host to a variety of important epiphytes which included *Gomphonema* spp., *Cymbella* spp., *Synedra* spp., *Cocconeis placentula* Ehr., *Diatoma vulgare* Bory, *Melosira varians* C. A. Ag., and *Audouinella violacea* (Kütz.) Hamel.

Growth of the supporting plant is of great importance to the epiphyte if the epiphyte is more or less restricted to this relationship (e.g., *Cocconeis placentula*, usually found in abundance only on *Cladophora* or *Oedogonium*), or when the growth of the epiphyte is greatly enhanced in the presence of large numbers of small irregularities in the attachment surface, such as is provided by small *Cladophora* plants (e.g., *Diatoma* and *Audouinella*, which colonize abundantly basal portions of *Cladophora* filaments). The growth of the epiphyte, likewise, can be of vital importance to the supporting plant, as in the case of the winter diatoms *Diatoma vulgare* and *Gomphonema olivaceum* (Lyngb.) Kütz., which grew so abundantly about the *Cladophora* filaments which they epiphytized, that they formed a cylinder as much as 4 mm. thick on all sides about the supporting filament. While it has not been demonstrated that these diatoms are responsible for the static winter condition of *Cladophora* in the Saline, such a relationship remains one of the more plausible explanations for this phenomenon.

Straining. — Large and small filamentous algae of all types function as traps for plankton and other sestonic materials. This straining process is of little importance in deep, slow-moving water. The layer of water moving across the riffles, however, is dispersed into a relatively thin sheet, all parts of which come repeatedly into contact with masses of benthic algae. These masses trap and strain out large numbers of living plankton organisms (CHANDLER 1937), thus reducing the reproduction within the stream of forms (*Dinobryon, Scenedesmus*) adapted to a planktonic existence, and providing a site for the reproduction and dissemination of essentially benthic forms such as *Oscillatoria tenuis* which, unable themselves to attach on the riffles, are nevertheless greatly benefited by the favorable conditions there, and grow locally in a luxuriant manner when by some external means they find anchorage.

THE ALGAL COMMUNITIES

While some doubt may be expressed concerning the applicability of the term, „community" to the algae of the potamoplankton, the term is acceptable when applied to unialgal, massive colonies, and such colonies are designated thus in the present work. An essentially

different treatment would be to consider such unialgal stands as seasonal aspects of a more permanent community. The latter treatment does not, however, express adequately the dominance which such massive growths manifest at certain seasons (e.g. the *Diatoma* and *Gomphonema* vegetations in winter); neither does it take into account the fact that they grow at levels essentially different from that of the permanent communities. In the Saline River these vegetations would, under such a system of nomenclature, become winter aspects of the permanent *Phormidium-Schizothrix* community. The latter association has already been described without reference to its winter aspect (FRITSCH 1949). On the other hand, BUTCHER (1932) has already described a winter *Diatoma-Gomphonema* community in a stream from which the *Phormidium-Schizothrix* is apparently absent. The writer prefers to regard these three units (1. *Phormidium-Schizothrix*, 2. *Diatoma*, 3. *Gomphonema*) as distinct communities until such time as they are shown to exhibit similar spatial relationships in other streams. Other comparable vegetations are also termed „communities" in this paper. It should be emphasized that the different units which are here termed „communities" are not necessarily of the same communal rank or importance.

Benthic Algae of the Unpolluted Portion

1. Permanent Crustose Communities

Phormidium-Schizothrix-Audouinella (Fig. 3). — This community is one of the most distinctive within the stream. It consists essentially of parallel filaments of *Schizothrix pulvinata* (Kütz.) Gom. and *S. lacustris* A. Br. mixed with larger filaments of *Phormidium incrustatum* (Nägeli) Gom. which have no definite orientation. The *Schizothrix* filaments are attached to the rock surface, to which they are more or less perpendicular. The *Phormidium* filaments are apparently not attached to the rock but lie more or less coiled or twisted within the matrix of closely packed filaments and sheaths, in part empty, of *Schizothrix*. Mixed with these three blue-green algae are branched plants of *Audouinella violacea* and *Cladophora glomerata*. This species of *Audouinella* is an almost constant member of this community and was found in about ninety-five per cent of the specimens examined. It is attached to the rock face directly, like the *Schizothrix*, and grows parallel to the latter and at a rate permitting the tips of its filaments to reach into the open water a slight distance beyond the tips of the *Schizothrix* filaments. The *Cladophora* is not a part of the community in the same sense as is *Audouinella*, for it is

found more often apart from the crusts of the *Phormidium-Schizothrix* community. Only minute basal cells of the dense *Cladophora* tufts are attached to or within the crust formed by the blue-greens. Many *Cladophora* plants are attached directly to the rock surface, frequently surrounded by, or piercing, this crust.

All parts of this community are encrusted with calcium carbonate which is deposited as a result of algal photosynthesis (PIA 1933, WELCH 1952). The carbonate deposits are found between the sheaths of *Schizothrix* and *Phormidium* and external to the filaments of *Audouinella*. The deposits must be removed by treatment with dilute acid before the algae can be studied microscopically.

Probably all members of this community are capable of growing alone without contact with either of the others. However, the *Phormidium* is seldom found in a pure state, and may be dependent on the presence of *Schizothrix* tufts for the development of its colonizing hormogonia. When the *Schizothrix* species are found almost alone, with a relatively small admixture of *Audouinella* and *Phormidium*, the crust formed is relatively thin and friable; with abundant *Phormidium* filaments in the ensemble, the crustose layer becomes more massive and more stony in consistency. Its surface is then much roughened and the crust may reach a total thickness of five millimeters. Such a development occurs only on riffles, although a thin crustose growth of *Schizothrix* species is fairly widespread in many pools with a rocky floor. *Audouinella* was frequently found growing alone, particularly in headwater riffles such as Station 5, and sometimes it grew epiphytically upon basal portions of *Cladophora*. Basal portions of both algae may become invested by a shell of calcium carbonate, but this deposit was never found on either alga for more than a few millimeters distal from its point of attachment.

The crustose structure here described is apparently identical with the *Phormidium-Schizothrix* community recently described by FRITSCH (1949, 1950) as occurring in certain calcareous British streams. Inasmuch as both British and American records are from streams high in lime, it is to be expected that calcareous streams of similar type in other parts of the world will likewise be found to possess such a community. We may infer from brief descriptions of KANN (1943), for example, that a similar community is to be found in many of the streams draining the north slope of the Austrian Alps in the basin of the Danube.

Development of the algae making up this community was followed upon sterilized rocks placed in the stream. Rocks placed in the stream on August 18, 1952, the earliest date upon which such rocks were placed on unpolluted riffles, had developed by December 15 minute, meagre growths of *Schizothrix* and *Audouinella*, only rarely admixed

with *Phormidium*. Even after twelve months in the stream, no structure at all comparable to the mature *Phormidium-Schizothrix* crust had been formed. Rocks placed in the stream after August 18, 1952 showed no colonization whatever by any of these algae throughout the fall and winter months. It may be concluded, therefore, that the mature crust such as is shown in Figure 3 requires a year or more for its development on a bare area. It may also be concluded that the six-month period of observation frequently employed by Butcher and other British workers, and based upon the removal at monthly intervals of slides anchored in the stream, is inadequate for the observation of successional changes leading to the development of a „climax" vegetation such as is found in this Michigan stream.

That the size of rocks colonized had any effect upon the formation of the *Phormidium-Schizothrix* community was not demonstrated clearly; however, careful search never revealed the presence of a mature, well-developed *Phormidium-Schizothrix* crust on rocks smaller than about 6 × 6 × 6 cm. On well-anchored but very small rocks, a crust of *Schizothrix* and *Audouinella*, as well as *Audouinella* tufts alone, could be found, but they were seldom mixed with *Phormidium incrustatum*. The rocks colonized by these algae were of widely different types, including limestone, gneiss, quartzite, granite gneiss, diabase, and mudstone. No differences in algal colonization or in algal vegetation as a result of the composition of the rock forming the substrate were ever observed. Furthermore, all of the attached species appeared to be capable of colonizing all rocks, indiscriminate of type, found on the stream bed.

That the volume of flow has some effect upon the *Phormidium-Schizothrix* community is possible, for it is never found in well developed condition in the headwater portion of the stream above Station 6. However, there are so many variables that change with distance along the river's course, that it is impossible to fix with certainty the cause of this phenomenon.

It is probable that a major portion of the growth of this complex algal layer takes place during specific seasons. Since its external changes were slow and difficult to observe, its periodicity, if any, was not investigated, and it is referred to here as a „permanent crustose community."

The *Phormidium-Schizothrix* community appears to represent the benthic climax on riffles, and is probably as clear an example of a climax community as this stream can offer. It occupied nearly all exposed rock surfaces on all unshaded rocky riffles in the course of the stream between Station 5 and Station 13. Other algae surpassed and shaded it at certain seasons, but these were only temporary species which disappeared from the stream after a few weeks or months of dominance. Between these seasons in which it assumed a secondary

role, the *Phormidium-Schizothrix* community remained the dominant and permanent occupant of the most desirable algal habitats. It may be compared with the eutrophic „climax" community of primary food producers in deep temperate lakes. However, the principal food producers in lakes are the phytoplankters (LINDEMAN 1942), a „life-form" which is of little importance on riffles, where the vast bulk of organic production must occur in the benthos.

In this connection, it may be stated that results of both chemical and biological studies of portions of the Saline River above and below Saline Pond indicated that eutrophy was greater below the pond and that production was correspondingly higher, a supposition which is borne out by the following facts: (1) that nitrates were consistently higher at Station 8 than at Station 5 above the pond; and (2) that growth of nearly all algae was distinctly more luxuriant at Stations 8 and 10 below the pond, than above the pond. These algae included (a) the *Phormidium-Schizothrix* community, which formed a thicker crust below the pond, (b) the winter diatoms *Diatoma vulgare* and *Gomphonema olivaceum*, and (c) *Cladophora glomerata* in spring. These observations may be considered as the basis for a hypothesis concerning the eutrophication of streams in general, namely that eutrophy of a lotic habitat may be brought about directly by an upstream pond or impoundment in which eutrophic conditions prevail. Too little is known of the processes of eutrophication in unpolluted streams to admit of general statements concerning the trophic evolution of a stream lacking impoundments. The conclusion, however, seems clear that the Saline Pond is instrumental in the eutrophication of habitats downstream from it, and that this pond-stream relationship may be of profound importance in streams generally.

Amphithrix-Gongrosira. — A second crustose community found on riffles in unpolluted portions of the river was made up of the blue-green alga *Amphithrix janthina* var. *torulosa* Gom. and the green alga *Gongrosira debaryana* Rabenh. Typically these algae formed calcified, cone- or cushion-shaped growths upon rocks, with filaments of both components radiating outward from the truncated point of the cone. Usually the shape of the colony is not evident without dissection, since the „cone" is often imbedded in the *Phormidium-Schizothrix* community with the surfaces of both communities confluent. Except for having a slightly greener color, and a less roughened surface, it resembles outwardly and appears to be a part of the dominant crustose community. Its composition was very constant, and the algae of the *Phormidium-Schizothrix* community seemed to be excluded completely from it, except in the very early stages of growth. Whether or not the *Phormidium-Schizothrix* community can overgrow it and destroy it, is unknown.

385

The *Amphithrix-Gongrosira* community was most conspicuous in September. In this month its dark green cushions could be observed widespread in swift water, on newly exposed or recently overturned rocks, and this is assumed to be its period of maximum growth. However, the cushions could be found in the stream at all seasons, and no data are at hand to show why or exactly when many colonies seemingly disappeared in the fall, nor to show the extent of the apparent seasonal change. Due to the close examination required to distinguish this community from the *Phormidium-Schizothrix*, and to its rather sporadic occurrence, it proved unfeasable to determine this community routinely in the field, and, hence, it was not recorded on the transects. It was never observed in the polluted portion of the stream.

Sterilized rocks placed in Riffle 8 on August 18, 1952, developed within eight weeks several colonies of *Amphithrix janthina* var. *torulosa*. Somewhat later, growths of colonizing *Schizothrix* and *Audouinella* were to be found. It appears, therefore, that these three genera represent pioneers in the succession which terminates in the full development of their respective communities. No further new colonization by *Amphithrix* was observed throughout the fall and winter months, and even eight months after the rocks had been placed in the stream, no growth of *Gongrosira* in the *Amphithrix* tufts was yet evident.

2. Summer Communities

Cladophora glomerata (L.) Kütz. — This was the most abundant and conspicuous filamentous alga in unpolluted parts of the Saline River, as it appears to be in most streams throughout the world. It is known to be highly sensitive to iron (BUDDE 1930, USPENSKI 1927) and relatively tolerant to high pH values (USPENSKI 1927). Numerous workers including PURDY (1930) and WASER, BLÖCHLIGER & THOMAS (1943) have observed that it is tolerant to relatively large amounts of sewage in the water. Its annual periodicity has been described by BROWN (1908) and BUDDE (1928, 1932). BROWN states that its maximum development is from April to June, whereas BUDDE describes a later maximum (May to August). Cladophoraceae are known generally to be absent from completely quiet waters (FRITSCH 1906), and JAAG (1938) states that development of *C. glomerata* is greatly dependent upon abundant light. Except as regards periodicity, results from the Saline River are largely in support of all these conclusions.

In the Saline River, *C. glomerata* was present in virtually all rocky riffles, as well as on rocks in shallow portions of pools (where its growth was greatly reduced) in all parts of the river above the in-

dustrial outfall at Saline. Between this outfall and Milan it was never observed in the river proper, although small plants were present in summer on rocks near water line in Milan Pond. Since no riffles are known to be present in the area between Mooreville and Milan, it may be supposed that its absence from the lower portion of this course was due to the lack of suitable riffles, but it is clear that its absence from the upper course between Stations 14 and 28, which includes numerous well developed riffles, is due to the affluents entering the river at Saline. Below Milan, a single riffle is known in the stream proper (Station 24); this was inhabited during the summer of 1952 by numerous small plants of *C. glomerata* mixed with other algae. The entire course of the stream between Saline and Milan from which *Cladophora* was absent has a total length of 21.0 km.

From the data available, it is impossible to establish with precision which of the components of the industrial effluent is responsible for the elimination of *Cladophora glomerata* from the stream. It seems probable that, in view of the extreme sensitivity of this species to iron, the iron content of this effluent would be sufficient to preclude any growth; very likely chromium, copper, or other „poisonous" ions entering the stream at this point would, even in the absence of iron, be sufficient to eliminate this species from the stream.

Another peculiarity in the distribution of *C. glomerata* in the stream was the presence of a few rather large plants at the crests of certain riffles while the species was greatly reduced or absent elsewhere on the riffle. This was usually the condition in unshaded riffles throughout the fall and winter period. There was no observable or measurable difference between upper and lower parts of the riffles except for a slightly higher current rate at the crest of the riffle. In an effort to explain this distribution on the basis of reduced amounts of dissolved oxygen in upper parts of the riffle, oxygen determinations were made at Station 8 throughout the night of August 2—3, 1952, at three points distributed in linear fashion from the upper parts of the riffle to its crest, where a few *Cladophora* plants were growing. Absolutely no consistent difference was observed in the amounts of dissolved oxygen when parts of the riffle were compared, although a significant difference was observed when the riffle was compared with the pool just beyond it. Some factor other than dissolved oxygen limits *Cladophora* to the crests of riffles at these stations in summer and fall.

Figures 9 and 10 show variation in important components of the vegetation at Stations 8 and 12, and are based upon transects made at approximately monthly intervals throughout the year. These records show that *Cladophora* plants are present throughout the year in unshaded riffles of the unpolluted portion. While minor pulses in the growth of *Cladophora*, occurring at various times of the year and

probably influenced by extended periods of sunny weather, are evident from such transect studies, the principal variation is more evident when dry weights of algae are compared on a month-to-month basis (Fig. 8). A period of rapid growth occurs in spring, values for which contrast sharply with the period of greatly reduced dry weight extending from summer or fall throughout the winter. The terminus of the spring period of maximum growth is much more poorly marked. Values for *Cladophora* at Station 8 (unshaded) were reduced sharply about four weeks after day temperatures of 15° were regularly attained in the stream, whereas at Station 5 (unshaded) the massive *Cladophora* vegetation was maintained for approximately three months after such temperatures were attained. It seems probable, therefore, that the summer decline in *Cladophora* which is here manifest is not due to lack of tolerance to higher temperatures, as is assumed by THURMAN & KUEHNE (1952).

There is at least one other way in which temperatures may be of importance in this problem, however. While there was no essential difference in day temperatures at Stations 5 and 8, there was a marked difference in night temperatures, with values at Station 5 unquestionably descending, for at least a few hours on cool summer nights, below 15°, whereas at Station 8 night temperatures are greatly moderated by the Saline Pond. It seems possible that the marked difference between the *Cladophora* vegetation at Stations 5 and 8 was due to the dependence of certain reproductive processes on at least short periods of cool temperatures. The only other consistent physico-chemical difference observed between these two stations in summer was the presence of small amounts of nitrate in the water at Station 8 and an almost total absence of nitrate at Station 5.

While it might be supposed that the rapid disappearance of *Cladophora* at Station 8 in June, 1952 was due to a period of high water and swift current at that time, the evidence from rainfall and water level (Fig. 5) gives no support to this supposition. Unfortunately, chemical data from this period are lacking, so that it is impossible to state whether or not any sharp changes in nutrients present in the water are correlated with this disappearance. Since the physical variables showed no significant changes at this time, the sudden reduction in *Cladophora* here cannot at present be correlated with any single environmental change.

The behavior of *Cladophora* at Riffle 12, which was heavily shaded in summer was, however, essentially different from its behavior in unshaded stations (Fig. 10). At Station 12, a marked spring growth of *Cladophora* took place as at other stations, but its rapid disappearance in June and July with the leafing out of overhanging and surrounding deciduous trees was striking and complete. No *Cladophora* whatever

was present in this riffle throughout a six-week period from July 20 to September 10, 1952 in sharp contrast to the condition at Stations 8 and 10, both of which showed a marked upsurge in *Cladophora* in mid-July. In late September, with the beginning of leaf fall, a meagre growth of *Cladophora* was found in scattered parts of the riffle, and for the remainder of the year the *Cladophora* vegetation was equivalent to that on the unshaded riffles. This behavior is in agreement with the observation of JAAG (1938) that a series of cloudy days suffices to reduce sharply the amount of *C. glomerata* in the upper Rhine.

Morphologic differences were evident between the fall or winter condition of the *Cladophora* plants and their condition for several days before detachment in late June. The characteristic glomerate plants were modified by the pronounced elongation (in May) of numerous main filaments and the detachment of the majority of the glomerate ends, giving the plants a stringy, fibrous appearance. Following a period of five to six weeks in May and June during which these fibrous skeins, which attain a length of one to two meters, virtually covered the floor of all riffles both shaded and unshaded, the plants detached by the breakage of a cell near the basal cell and were, of course, immediately carried downstream, leaving behind on the rock only the minute basal filaments of relatively few cells. Since the much elongated skeins meanwhile become intricately tangled by water currents with other *Cladophora* plants growing around them, the detachment of one plant may occasion a simultaneous removal of many plants from a given portion of the riffle. The sudden disappearance in this way of the massive spring *Cladophora* vegetation left the riffle relatively bare except for the widespread crustose communities, which thus became suddenly exposed after remaining in heavy shade throughout the late spring. Limited growth of *Cladophora* may apparently take place at any time from the remaining basal filaments, and glomerate portions of such of these small plants as remain in late winter presumably produce a spring crop of gametes and zoospores.

According to LIST (1930) zoospores of *C. glomerata* are liberated throughout almost the entire year, but available evidence indicates that such may not be the case in the Saline River. Abundant colonization by *Cladophora* on sterilized rocks placed in the river at Station 8 occurred between August 18 and September 23, 1952, but no further colonization whatever was observed on such rocks throughout the fall and winter period, in spite of the continued presence of numerous well developed and glomerate, albeit small, plants on this and upstream riffles.

There appears to be no limit at either end of the scale to the size of rock upon which motile cells of *Cladophora* can establish themselves. All of the largest boulders in the unpolluted riffles showed good

growth of *Cladophora* in May and June, 1952, and well developed plants with attached basal cells were found on rock particles so small as to weigh only about fifty milligrams when dried. Small rock particles were seldom found exposed on the bed of a riffle, and would, of course, be unable to provide anchorage there for any alga, but such particles are abundantly found enmeshed within the masses of large *Cladophora* plants, and many are utilized for the attachment of germlings of the same species. A large plant of *Cladophora* in spring or summer acquires a host of such rock particles, and through the germination of motile reproductive cells within the relatively quiet water at the center of the mass of filaments, comes to serve as a veritable marsupium for the growth of innumerable offspring of itself or of upstream plants. All such younger individuals are, of course, doomed to become river debris upon the detachment of the encompassing parent.

Lyngbya aestuarii (Mert.) Liebm. — This blue-green alga grew inconspicuously at Station 8 and was occasionally recorded from other unpolluted riffles. It forms a whitish, cobwebby net over the surface of the *Phormidium-Schizothrix* crust, on a few scattered rocks. The whitish color of this net is due to the heavily calcified sheaths which surround and enclose the blue-green trichomes. *Lyngbya aestuarii* was known to be present from July through September, and was absent in the fall and winter months, but the dates of its appearance and departure were not determined precisely.

Oscillatoria Community. — In the Saline River this benthic community is dominated by *Oscillatoria tenuis* Ag. In early summer it was found widespread on pool bottoms where even a small amount of silt had accumulated, the *Oscillatoria* penetrating the upper layers of silt and trapping more mineral particles among the exposed filaments. The complex of *Oscillatoria* and silt thus constituted permits the growth of numerous algae mixed in with *O. tenuis*. These include:

Merismopedia convoluta Bréb.
Oscillatoria princeps Vauch.
Spirulina major Kütz.
Pediastrum duplex Mayen
Scenedesmus abundans (Kirch.) Chod.
Scenedesmus arcuatus var. platydisca G. M. Smith
Ankistrodesmus falcatus (Corda) Ralfs
Euglena oxyuris Schmarda
Cymbella spp.
Navicula cryptocephala var. intermedia Grun.

This community was first evident in late May on silty banks in shallow portions of pools. Eventually, it spread over the entire pool bottom and to shady portions of the riffles. By touching bottom

with a pole, it could easily be dislodged in large or small masses which then floated to the surface and moved downstream. As described above, the masses of *Oscillatoria* with their contained silt and other algae are naturally torn from the bottom when at midday or thereabouts sufficient oxygen becomes trapped in the reticulum of filaments to overcome the weight of the mass of silt. Unlike *Cladophora* plants, which, once dislodged, are usually unable to grow successfully where they become snagged downstream, the *Oscillatoria* and other algae entrapped in its meshes profit from this dislodgment to propagate themselves over the entire downstream area which is ecologically adapted to their growth. Although sufficient quantities of the *Oscillatoria* community arrived daily throughout July as far downstream as Station 18 to ,,seed'' the polluted course of the stream, only *Euglena oxyuris* and *Navicula cryptocephala* were ever found below Station 14 in such a condition as to suggest their successful growth; none of the other species typical of the *Oscillatoria* community survived the heavy concentration of pollutants at Stations 14 and 15.

A growth maximum was reached by *O. tenuis* in July and August, 1952. The season of this maximum agrees in general with a similar maximum recorded by BUTCHER (1924). Although this species disappeared from the riffles of the Saline shortly after this time, it remained on certain shaded banks in the unpolluted portion of the river until late in October. The growth of *O. tenuis* in pools seemed to be consequent upon its sensitivity to bright light, for on riffles it grew conspicuously only in markedly shaded situations. *O. tenuis* did not develop massively in 1953.

Spirogyra Communities. — None of the numerous species of *Spirogyra* found in the stream was ever found in fruiting condition throughout the period of this study and the writer was unable to induce fruiting in the laboratory. The species were therefore not determinable, with the exception of *S. fluviatilis* Hilse which occurs in the Saline, as it probably does in the majority of streams in northeastern United States, and is almost surely recognizable in vegetative condition from the fact that it is one of the very few attached Spirogyras. Numerous other species of *Spirogyra* were found in the unpolluted course of the stream. Usually they occurred as floating inhabitants of quiet, very shallow, water at the side of riffles or pools, or on shoals where the deposits of silt and contained organic material provide abundant nutrients. These species frequently grow together in such a way that the visible mass of filaments is a complex of three or more species. Local growth may be surprisingly fast in these algal masses at certain periods, and the disappearance may be equally rapid and superficially inexplicable. After an initial attempt to record the comings and goings of such *Spirogyra* communities in the

summer months, observations were reduced to frequent collections from the principal stations.

Summer diatom communities. — Various diatoms were found abundantly in the River throughout the summer as benthic algae both in riffles and in pools. The most important are listed below:

Synedra ulna (Nitzsch) Ehr.
Synedra acus Kütz.
Cymbella prostrata (Bréb.) Cl.
Cymbella affinis Kütz.
Cymbella tumida Van H.
Cymbella ventricosa Kütz.
Navicula viridula Kütz.
Navicula cryptocephala Kütz.
Navicula cryptocephala var. intermedia Grun.
Navicula gracilis Ehr.
Melosira varians C. A. Ag.

Such diatoms usually occurred in mixtures of various species, forming a brown layer on silty banks or on protected portions of rocks. *Cymbella prostrata* formed the most conspicuous summer growths, which somewhat resembled the winter vegetation dominated by *Gomphonema olivaceum*. The impossibility of determining macroscopically the diatom species contained in these homogeneous brown layers rendered necessary the recording of the diatoms as a group in the transect studies at certain times and places. Starting in late September it became possible to distinguish one species, *Diatoma vulgare*, which from that time on dominated and eclipsed all other diatoms on riffles. The equally distinctive *Gomphonema olivaceum* was also recorded by name after its appearance in late November.

3. Winter Communities

The *Diatoma-Gomphonema* „community" (BUTCHER 1932) is really composed of two distinctive and competitive algae whose growth maxima do not coincide. The first of these to appear, *Diatoma vulgare* Bory, grew in extremely dense stands of short filaments on rocks in riffles. Its distribution in space was intriguing: in winter it was dominant in unpolluted riffles below Saline Pond, whereas it was absent as a dominant alga in all known riffles of the stream proper above the pond. In certain of the upper tributaries, however, particularly Tributary 11, it was very abundant, a condition which contrasted in striking manner with that at Station 5, immediately below the mouth of this tributary, where little of the *Diatoma* was to be found. In seeking the cause for this peculiarity of distribution, it was found that both Tributary 11 and Stations 8—12 maintained rela-

tively high concentrations of nitrate throughout the winter, whereas Station 5 remained somewhat poorer in nitrates (Fig. 7). Apart from this difference in nitrate content, no significant physico-chemical differences in the water between Stations 5 and 8 could be observed by the procedures employed.

Diatoma community. — Colonies of *Diatoma vulgare* were common in polluted riffles of the Saline River in winter but nowhere did it achieve dominance as in the unpolluted stations. In streams of Thuringia, KOLBE (1932) described a spring maximum of *Diatoma vulgare*. The *Diatoma* vegetation of the Saline River rose to dominance in the autumn of 1952 as soon as water temperatures had fallen below about 15° centigrade (Figs. 4, 9, 10). Throughout the early winter period, the dominance of this form was uncontested on riffles below Station 7. As the winter progressed, colonies of *Gomphonema olivaceum* gradually but surely took over the sites occupied by *Diatoma*, and by February 15, 1953, had largely replaced the latter. When in early spring this *Gomphonema* vegetation waned, *Diatoma* returned briefly to dominance, exhibiting good growth for a few weeks in April, and finally disappeared as an important unit of the vegetation around June 1.

Gomphonema community. — The other principal diatom of the winter period, *Gomphonema olivaceum* (Lyngb.) Kütz., grows massively in colonies with the individual cells attached at the ends of minute, ramifying pedicels. The confluent pedicels form conspicuous masses of gelatinous material as much as one centimeter in thickness on exposed rocks. This species was common on riffles and co-dominant in late winter throughout the unpolluted portion of the river. Although it could be found in winter in polluted portions of the river, its colonies there remained small and did not become macroscopically visible until late in March. In Holstein, RAABE (1951) has found this diatom reaching its maximum in March.

The growth of *Gomphonema* in the Saline River was luxuriant in late February and approximately as massive as the *Cladophora* vegetation of late May. Its disappearance corresponded with the general rise in water temperature in mid-April. Isolated cells of both *G. olivaceum* and *Diatoma vulgare* could, however, be found throughout the year. The detachment and disappearance of *Diatoma* was slow and imperceptible due to the small size of the individual *Diatoma* filaments. The tan-colored colonies of *Gomphonema*, however, detached and floated downstream conspicuously in large gelatinous masses, starting about February 15 (vide BLUM 1953).

Abundant reproduction was exhibited by *Diatoma* throughout early winter. All sterilized rocks placed in the riffles between October 27 and March 1 were quickly colonized by this alga, often so rapidly

that the new colonies were visible to the eye within ten days. Colonization by *Gomphonema* was equally rapid, but did not begin until about November 25. From this date on through February 15, all sterilized rocks placed in the stream soon acquired new colonies of both principal diatoms and little else.

Batrachospermum boryanum Sirod. — This freshwater red alga is common in late winter and early spring in the headwaters of Tributary 15 as well as at Station 10 and 12 in the river itself. It has never been found below Station 12. It grows attached to rocks in a manner similar to *Cladophora glomerata*. Its growth is slow and is greatly enhanced by a certain amount of shade, as in other members of this genus. In this connection, it is interesting to note its virtual confinement to the shaded portions of Tributary 15 and to the heavily shaded Station 12 in the Saline River system, in spite of the fact that the erect portion of the alga grows only in the cold season when the protection offered by surrounding trees is in part removed by the temporary absence of leaves.

The first erect portions of *Batrachospermum* made their appearance in mid-November. They grew slowly throughout the winter, attaining a maximum size about April 1. Presumably the growing season is climaxed at least in some plants by sexual reproduction and cystocarp formation. The only cystocarpic material found in the Saline was collected at Station 12 on May 9, 1953. With the advent of higher water temperatures, the erect portions detached and disappeared, with some individuals remaining in place until about May 20. None of the sterilized rocks placed in the stream at intervals from August 22, 1952, on showed any production of erect portions of *Batrachospermum* in the winter of 1952—53.

Ulothrix tenuissima Kütz. — This alga grew abundantly at water line on rocks in the shaded riffle 12 throughout the late winter period. It was also observed in a few shaded situations at Station 8, as well as in certain tributaries, during the same season. It was never found in the polluted portion of the stream.

4. Other algae

In addition to the algae discussed above, vegetative material of *Spirogyra*, *Zygnema*, *Mougeotia*, and *Oedogonium* was found commonly in unpolluted portions of the stream. Other algae collected from these portions are listed below:

Euglena oxyuris Schmarda
Merismopedia tenuissima Lemm.
Merismopedia glauca (Ehrenb.) Näg.
Merismopedia convoluta Bréb.

394

Entophysalis rivularis (Kütz.) Dr.
Spirulina major Kütz.
Oscillatoria princeps Vauch.
Phormidium autumnale (Ag.) Gom.
Phormidium retzii (Ag.) Gom.
Calothrix braunii Bornet & Flahault
Stigeoclonium tenue Kütz.
Draparnaldia plumosa Ag.
Chaetophora elegans Ag.
Chaetophora pisiformis Ag.
Schizomeris leibleinii Kütz.
Coelastrum microporum Näg.
Scenedesmus dimorphus (Turp.) Kütz.
Scenedesmus abundans (Kirch.) Chod.
Scenedesmus arcuatus var. platydisca G. M. Smith
Scenedesmus quadricauda (Turp.) Bréb.
Pediastrum tetras var. tetraedon (Corda) Rab.
Pediastrum integrum Näg.
Pediastrum duplex Mayen
Pediastrum duplex var. cohaerens Bohlin
Ankistrodesmus falcatus (Corda) Ralfs
Rhizoclonium hieroglyphicum Kütz.
Chara contraria A. Br.
Asterocytis smaragdina Reinsch
Vaucheria schleicheri de Wildeman
Tribonema minus West
Tribonema bombycinum Derbès & Solier
Dinobryon divergens Ehr.
Dinobryon bavaricum Pascher.

Benthic Algae of the Polluted Portion

1. Permanent Crustose Communities

Navicula atomus (Näg.) Grun. — This extremely minute diatom had an interesting distribution: it was found nowhere in the unpolluted portion of the stream, but appeared to be present on virtually every rock in the stream below the industrial outfall at Saline for at least 3.2 km. downstream. It was not confined to riffles, although its best growth was made in riffles. It was found only on rocks or other permanent supports, and as it can apparently secrete abundant limy material, it comes in time to form calcareous layers of cons derable thickness on the supporting rock. As new diatom cells are formed by division, the cells adjacent to the rock become buried and fossil-

ized in a slowly accumulating deposit of calcium carbonate. These crusts measured up to three mm. in thickness. The outer layers of the crust were usually brighter green than the inner, indicating the greater abundance of living cells in the outer layers. Throughout much of the year, the crust was covered over and hidden by the heavy growths of *Nitzschia palea*, *Stigeoclonium tenue*, *Sphaerotilus natans*, or other algae of the heavily polluted portion. When one or another of these superficial algae experienced widespread removal from its substratum, the *Navicula* vegetation became momentarily visible until such time as it again became covered by silt, by new growth of diatoms, or by regeneration of the superficial algae.

The *Navicula atomus* layer was present throughout the year and showed little if any seasonal fluctuation in amount.

2. Summer Communities

Stigeoclonium tenue Kütz. — This is the largest alga in the polluted course of the river. Its branched filaments form long, massive, almost fluid streamers in riffles throughout much of the year. Like *Cladophora*, it is never found in entirely quiet water. Remarkably enough, it can resist the pull of water currents up to 1.35 m. per second. At Station 14, immediately below the industrial outfall at Saline, its spring growth was more luxuriant than at any other known point in the river. At this place and time, numerous plants 0.40—0.50 meters in length could be seen. Downstream from this point, its growth was less massive, and the amount of *Stigeoclonium* bore, in rough terms, an inverse relationship to the distance from the Saline outfalls. Thus, at Station 25 at Saline Mills, a good summer growth consisting of many large plants could be found, whereas at Station 28 only much smaller plants were present, and growth of these, moreover, was greatly restricted in time. Below this point, due in part to the absence of suitable riffles, *Stigeoclonium* was much less abundant. This alga was not confined to polluted portions of the river, but its occurrence above the polluted course of the river was, by contrast, highly sporadic.

In general, good growth of *Stigeoclonium tenue* was limited to the warm months. Small plants were, however, abundant in winter at certain stations, although throughout much of the winter the alga was completely missing at Station 14, where its best spring growth was attained. Its periodicity can best be discussed by reference to the individual stations in order:

Station 14 (Fig. 11). In late winter no erect portions of *Stigeoclonium* were present. In May of both years there occurred a notable upsurge of great magnitude. This was followed in June, 1952, by a

marked reduction, which did not occur in 1953. Subsequent increases occurred early in August and in mid-September, 1952, each followed by periods of decline. In early October, 1952, a more permanent decline set in, and few or no plants were to be found throughout the winter.

Stations 15 and 18 (Fig. 12). These two heavily polluted stations behaved more or less as a unit throughout the period of the study. In late winter, small *Stigeoclonium* plants appeared at the crests of these riffles, but the remainder of each riffle was almost devoid of *Stigeoclonium*. A great development of this alga took place in May as at Station 14, but in Stations 15 and 18 *Stigeoclonium* was quickly overgrown and replaced, about July 1, by vigorous growth of *Sphaerotilus natans* Kütz. Throughout the warm months, *Sphaerotilus* was dominant on both these riffles, with only a few *Stigeoclonium* plants retaining a foothold at the crests of riffles where the current velocity appeared to be a limiting factor for the heavy and extremely fragile thalli of *Sphaerotilus*. With the widespread detachment of *Sphaerotilus* as soon as water temperatures fell below about 15° C., *Stigeoclonium* experienced a brief and moderate recrudescence, but again fell off to virtual disappearance in the latter part of December.

Station 25. This station, at a distance of 1.6 km. below the Saline outfalls, had at least a reduced vegetation of *Stigeoclonium* throughout the year, even in winter months when *Stigeoclonium* was practically or entirely wanting at Stations 14, 15, and 18. The small plants present here in March and April grew rapidly in May to their maximum size as at the upstream stations cited. At Station 25 in 1952 and 1953 a marked reduction occurred, however, only in July, and came at a time when the *Stigeoclonium* at Station 14 was in full development. This regression was followed in 1952 by two periods of marked growth, each followed by a decline. The first of these growth periods reached a climax in late August, the second in mid-September. Later in September, well before a similar decline at Station 14, the *Stigeoclonium* vegetation fell off to a few small plants which remained, however, in good condition throughout the winter.

Station 28 (Fig. 13). Growth of *Stigeoclonium* at this station, at a distance of 3.2 km. below the Saline outfalls, was greatly curtailed by comparison with upstream stations. Throughout much of the year, rocks in this riffle were covered with a dwarf form of *Stigeoclonium*. While no development of the usual erect plants took place throughout most of the year, rapid, widespread growth of these plants occurred in August, 1952, and in May and June, 1953. At these times the entire riffle floor within a fortnight developed a massive *Stigeoclonium* vegetation with plants up to 0.40 m. in length. This vegetation was ephemeral, however, and disappeared within a few weeks

397

more quickly than it had come. This disappearance, in 1952, coincided precisely in time with the regression in *Stigeoclonium* at Station 25, but at Station 28 it was complete, no erect portions of plants whatever remaining in the stream. The disappearance did not correspond in either year with any apparent reduction in the co-dominant *Nitzschia* vegetation. After September 18, 1952, no further *Stigeoclonium* was to be found in the stream at this point throughout the remainder of that year. The changes shown in figure 13 are based on rough visual estimates, as transects were not made at this station.

Convincing evidence of correlation between the disappearance of *Stigeoclonium* and conditions within the stream was not obtained. The disappearance of *Stigeoclonium* at Station 28 long before its permanent reduction elsewhere is noteworthy and unique, but the general reduction at Station 14 and 25 in early October can conceivably be correlated with a variety of environmental changes occurring at this time.

Nitzschia palea (Kütz.) W. Smith. — While this species was not confined, like *Stigeoclonium tenue*, to rapidly moving water, it was co-dominant on riffles (with *S. tenue*) in the polluted course of the river. It was able, along with *N. linearis* W. Smith, which accompanied it, to maintain its position and to reproduce in late summer in water moving at a rate of at least 0.40 meters per second. Where it grew in abundance, it formed a rich brown calcareous layer as much as one millimeter in thickness, on rocks on sandy or gravelly portions of the bottom (thus somewhat consolidating the bottom), or on mats of *Sphaerotilus*. It grew everywhere in very shallow water, from the water's edge to a depth of about ten centimeters; hence it was especially conspicuous on shoals, in shallow backwater areas, and in riffles. It was lacking from heavily shaded areas.

This species was found sparsely above the Saline outfalls, but its massive growth, accompanied by *N. linearis*, occurred only in the polluted portion. Immediately below the industrial outfall at Saline, in fact, colonies of this alga were conspicuous on bottom sand in August and September. In shallow water in the entire course of the stream beyond this point, as far downstream as Station 32, its growth was prodigious.

N. palea is a familiar inhabitant of the α- and β-mesosaprobic zones of polluted streams (MARSSON 1908, BUDDE 1930, KOLBE 1932, BUTCHER 1949, HORNUNG 1951). Like other algae of the polluted zone of the Saline River, it can apparently tolerate relatively large amounts of copper (cf. SCHRÖDER 1939) and chromium.

This species was conspicuous in the stream only in the warm months (Fig. 13). It was first seen in June, 1952, and increased rapidly at all observed points throughout late June and early July. A marked

decline occurred in late July; this was followed by a period of very rapid growth in August. Throughout much of August and all of September, *Nitzschia* was more conspicuous than any other alga, and probably exceeded all other algae in dry weight.

After this period of dominance, the *Nitzschia* vegetation disappeared in early October with great rapidity. At most observed stations this decline began at approximately the same time but was completed more rapidly at Stations 25 and 28 than at Stations 14 and 38. As with the almost simultaneous reduction in *Stigeoclonium tenue* at Station 25, this decline may be correlated with numerous environmental changes, any one of which may be responsible for it.

In 1953 *Nitzschia palea* again became conspicuous in June. At Station 25 an apparent maximum growth was reached in late July. At Station 28 this condition was delayed until late August.

Spirogyra spp. — Numerous species of *Spirogyra* inhabited pools, shoals, and backwater areas of the polluted portion of the River. As in the upper course, *S. fluviatilis* was common on rocks and silt-covered banks in shallow water, thus showing little or no response to the pollutants entering at Saline. In addition, several other unattached species were present and grew luxuriantly in summer on the bottom or just above the bottom. Throughout late summer and much of the autumn of 1952, certain of these *Spirogyra* species grew rapidly in the extensive pool found below Station 15 and just below the sources of pollutants where the concentration of organic material, as well, presumably, as of the metallic poisons, was greatest. It appeared possible that this pool was the center of dispersal for *Spirogyra* to much or all of the remainder of the stream. *Spirogyra* was first observed here in quantity in mid-June, and early in July the mechanism of dispersal from shoals which is described above (Fig. 2) was already in operation at this station. From this time on, every day of fair weather witnessed the rising and movement downstream of masses of living filaments, each carrying a portion of the silty stream bottom which was torn away by the disengagement of the algal mass. In this way the algae unquestionably played a considerable role in the transport downstream of undecomposed solids and, hence, in the self-purification of the stream.

Consequent upon the massive reproduction of *Spirogyra* within this pool in the summer, the filaments eventually spread downstream as if overflowing the pool, and both attached and unattached masses were recorded on transects made at Station 18 in July, August, and September, 1952. Abundant filaments could sometimes be found growing on the riffle and surrounded by *Sphaerotilus* tufts.

The benthic masses of *Spirogyra* remained in mid-current in this pool, somewhat reduced in the autumn months, until about January

1, 1953, when the last of these masses disappeared. The *Spirogyra* masses in the shallow backwater areas at this station never entirely disappeared throughout the period of this study.

Closterium-Euglena community. — In a stream bearing sewage, silt banks in areas of quiet water are extremely rich in organic materials. As the bank builds up by sedimentation, thick deposits of black mud are formed. These deposits, along with other environmental factors (such as abundant light, water which is constantly but slowly replenished, and high temperatures, and poisonous substances of industrial origin) which operate on such shoal areas, permit the growth of a limited number of algae, but these grow luxuriantly, forming small green patches on the silt. The *Nitzschia* species characteristic of this portion of the river in the entire course from Station 15 to Station 28 formed an ubiquitous background for these green colonies and were mixed invariably with the other algae forming the colonies. These other algae included particularly the following:

Closterium acerosum (Schrank) Ehr.

Euglena acus Ehr.

Euglena oxyuris Schmarda

Navicula cuspidata Kütz.

This vegetation was not as widespread as the *Spirogyra* or the *Nitzschia* vegetation, although its development was approximately synchronous with that of the latter. The *Closterium-Euglena* vegetation was at its maximum density in August and September, 9152. It disappeared in the first week of October at the same time as, and possibly in response to the same environmental changes that induced, the reduction in the *Nitzschia* vegetation.

3. Winter Algae

Diatoma vulgare Bory — This diatom, so characteristic of the fall and winter months in the unpolluted riffles, was found throughout the latter months of winter in all the polluted riffles but in exceedingly reduced amount, constituting probably less than one per cent of its production per unit area in upstream riffles. Its habit of growth was likewise somewhat different in polluted stations: instead of forming filaments 1—2 centimeters in length, it formed minute tufted colonies or masses not more than 2—3 millimeters in length. Its development in polluted riffles was, moreover, slower than in upstream riffles; at Station 8 (unpolluted), for example, *Diatoma* achieved virtually its maximum development by October 20, whereas at Station 18 (polluted) this was not achieved until about November 25. Its usual substrate in polluted situations was living or moribund filaments of *Stigeoclonium*, or the mats of *Sphaerotilus* which

it colonized extensively, or, as in upstream stations, the rocks of the stream bottom.

Tetraspora sp. — This alga, found only rarely in upstream situations, was characteristic in late winter of the polysaprobic riffles 15 and 18 where it formed globose or cylindric colonies about one centimeter in diameter. Here it was limited, more so than any other alga in the stream, to the downstream, protected faces of rocks in the riffle. In the β-mesosaprobic Stations 25 and 28 this species was present throughout much or all of the year. On occasional visits, no *Tetraspora* could be found, but it was nevertheless recorded in practically every month of the year from both stations.

Euglena spp. — Throughout autumn and early winter, areas several square centimeters in extent near Stations 14, 15, and 18 were frequently covered by conspicuous green sheets which, upon examination, proved to be composed entirely of *Euglena* species, especially *Euglena sociabilis* Dangeard and *E. viridis* Ehrenb. Such abundant growth of *Euglena* was not observed in downstream stations until January 23, 1953, when a massive *Euglena* population was discovered covering the entire river bottom, with the exception of riffles and of deep water in midstream, from Station 15 to Station 38 and beyond, a distance of more than 17 km. Numerous species, including *E. sociabilis*, *E. viridis*, *E. stellata* Mainx, *E. chadefaudii* Bourrelly, and *E. schmitzii* Gojdics, were mixed in. This conspicuous growth of *Euglena* remained, somewhat reduced in amount after February 1, until about March 15, at which time its extent had diminished, and become inconspicuous as in much of the fall and early winter.

Plankton Algae

The phytoplankton of the Saline River reflected in general the organisms present on the bottom, although the larger algae such as *Cladophora* and *Spirogyra* were as a rule not adequately represented. The plankton was not sampled at regular intervals, but it was evident from the few samplings scattered throughout the year that great variations both qualitative and quantitative obtained in the plankton as in the bottom organisms.

Series of plankton samples were taken on July 21, August 18, October 16, 1952, and January 16, 1953. The July sampling contained in small amount representatives of the *Oscillatoria* vegetation of the unpolluted stations, and, in material from the polluted stations 15 and 28, a high concentration of *Nitzschia palea*. Upstream stations in the August sampling showed relatively few cells, but in the samples from polluted stations the massive benthic vegetation of *Nitzschia palea* was clearly reflected, the maximum concentration of *Nitzschia*

being recorded at Station 28 (450,000 per liter) with stations further downstream exhibiting a marked reduction in *Nitzschia* (to total absence at Station 34). On October 16 the plankton everywhere was greatly reduced by comparison with the August sampling. Insignificant amounts of plankton organisms were present at unpolluted and polluted stations with the exception of Station 32, where significant amounts of *Synedra acus* Kütz. were present (214,000 units per liter), as well as considerable amounts of *Nitzschia palea*. Results of the January samplings showed essentially minimal numbers of phytoplankton organisms at all stations.

The plankton of the Saline River showed, in the portion investigated, no essential conflict with BUTCHER's conclusion (1932) that small streams generally lack a plankton distinctive from, and over and above, their benthic organisms. All of the common plankton algae observed in the Saline, with the exception of the October plankton of *Synedra acus*, and of those forms which clearly originated in an impoundment such as Saline Pond, were obviously of benthic derivation.

SUMMARY

1. The algal vegetation of the Saline River, Michigan, U.S.A. was studied throughout a period of eighteen months in 1951—53, with exact qualitative and quantitative records maintained throughout a fourteen-month period. Determinations were made at regular intervals of a variety of environmental physico-chemical variables which may be supposed to influence algal growth.

2. The upper course of the Saline River is unpolluted and mildly alkaline, has a high bicarbonate content, usually abundant nutrients, and has an algal vegetation which includes *Cladophora glomerata* in spring, *Diatoma vulgare* and *Gomphonema olivaceum* in winter, and a calcified *Phormidium-Schizothrix* community which is present throughout the year.

3. The lower course of the river was influenced by industrial wastes and sewage entering the river principally at Saline and Milan. Below the industrial outfall at Saline the water contained chromium, and other toxic ions, and the flora of the upper course had disappeared almost entirely, being replaced by a luxuriant flora of *Stigeoclonium tenue* and other species. Below the domestic outfall at Saline, the summer riffle vegetation was dominated by the bacterium *Sphaerotilus* and the diatom *Nitzschia palea*; at other seasons *Stigeoclonium tenue*, *Tetraspora*, and *Navicula atomus* were present on riffles whereas the pools were dominated by *Spirogyra* spp.

4. No marked change was observed in the flora of the middle course

of the stream between Saline Mills and Milan. Below Milan, *Clado-phora* returned to the stream flora within a single riffle. A massive accession of sewage at Milan polluted the stream again at this riffle, and the stream remained polluted for the remainder of its course.

5. The periodicity of the principal algae is described and is summarized in figures 8—13.

6. The following organisms are markedly resistant to the presence of chromium and other polluting ions; possibly also they profit from the presence of one or more of these pollutants: *Stigeoclonium tenue, Tetraspora sp., Closterium acerosum, Nitzschia palea, N. linearis, Navicula atomus, Navicula cuspidata, Euglena sociabilis, E. viridis, E. acus, E. oxyuris, E. stellata.*

BIBLIOGRAPHY

ALLEN, W. E. - 1920 - A quantitative and statistical study of the plankton of the San Joaquin River; *Univ. Cal. Public. Zool.* 22: *1—292*, Pl. 1—12.

BAY, J. W. - 1938 - Glacial history of the streams of southeastern Michigan; *Cranbrook Inst. Sci. Bull.* 12, 68 p. Bloomfield Hills.

BLUM, J. L. - 1954 - Two winter diatom communities of Michigan streams; *Pap. Mich. Acad. Sci., Arts, Lett.* 34: *3—7* (1953).

BROWN, H. B. - 1908 - Algal periodicity in certain ponds and streams; *Bull. Torrey Bot. Club* 35: *223—248*.

BRUJEWICZ, J. - 1931. Tägliche Schwankungen der hydrochemischen Faktoren im Flusswasser; *Verh. Int. Ver. Theoret. Ang. Lim.* 5: *442—457*.

BUDDE, H. - 1928 - Die Algenflora des Sauerländischen Gebirgsbaches; *Arch. Hydrobiol.* 19: *433—520*.

——— 1930 - Die Algenflora der Ruhr; *Arch. Hydrobiol.* 21: *559—648*.

——— 1932 - Limnologische Untersuchungen niederrheinischer und westfälischer Gewässer. Die Algenflora der Lippe und ihrer Zuflüsse; *Arch. Hydrobiol.* 24: *187—252*.

BUTCHER, R. W. - 1924 - The plankton of the River Wharfe; (Yorkshire) *Naturalist* 1924: *175—180, 211—214.*

——— 1932 - Studies in the ecology of rivers. II. The microflora of rivers with special reference to the algae on the river-bed; *Ann. Bot.* 46: *813—861.* Pl. 33—34.

——— 1940 - Studies in the ecology of rivers. IV. Observations on the growth and distribution of the sessile algae in the River Hull, Yorkshire; *J. Ecol.* 28: *210—223.*

——— 1949 - Problems of distribution of sessile algae in running water; *Verh. Int. Ver. Theoret. Ang. Lim.* 10: *98—103.*

———, PENTELOW, F. T. K., and WOODLEY, J. W. A. - 1930 - Variations in the composition of river waters; *Int. Rev. Ges. Hydrobiol. Hydrogr.* 24: *47—80.* 1930.

CHANDLER, D. C. - 1937 - Fate of typical lake plankton in streams; *Ecol. Monogr.* 7: *445—479.*

EDDY, S. - 1932 - The plankton of the Sangamon River in the summer of 1929; *Bull. Ill. State Nat. Hist. Surv.* 19: *469—486.*

FEIGL, F. - 1937 - Qualitative analysis by spot tests. ix, 400 pp. Elsevier.

FISKE, C. H., and SUBBAROW, Y. - 1929. Phosphocreatine; *J. biol. Chem.* 81: *629—679.*

FRITSCH, F. E. - 1906 - Problems in aquatic biology, with special reference to the study of algal periodicity; *New Phytol.* 5: *149—169*.

—— 1949 - The lime-encrusted *Phormidium*-community of British streams; *Verh. Int. Ver. Theoret. Ang. Lim.* 10: *141—144*. Pl. 2.

—— 1950 - *Phormidium incrustatum* (Näg.) Gom., an important member of the lime-encrusted communities of flowing water. *Biol. Jaarboek* 17: *27—39*. Pl. 1, 2.

HORNUNG, H. - 1951 - Biologischer Nachweis der Verunreinigung der Echaz durch Abwässer; *Veröff. Landesst. Naturschutz Würtemberg-Hohenzo lern* 1950: *272—280*.

JAAG, O. - 1938 - Die Kryptogamenflora des Rheinfalls und des Hochrheins von Stein bis Eglisau; *Mitt. Naturf. Ges. Schaffhausen* 14: *1—158*. Pl. 1—18.

KANN, EDITH - 1943 - Krustenalgen in Alpenbächen; *Arch. Hydrobiol.* 40: *459—473*.

KOCH, F. C., and McMEEKIN, T. L. - 1924 - A new direct nesslerization micro-Kjeldahl method and a modification of the Nessler-Folin reagent for ammonia; *J. Amer. Chem. Soc.* 46: *2066—2069*.

KOFOID, C. A. - 1903 - The plankton of the Illinois River, 1894—1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part 1. Quantitative investigation and general results; *Bull. Ill. State Lab. Nat. Hist.* 6: *95—629*. Pl. 1—50.

—— 1908 - The plankton of the Illinois River, 1894—1899. Part II. Constituent organisms and their seasonal distribution; *Bull. Ill. State Lab. Nat. Hist.* 8: i—vii, *1—355*. Pl. 1—5.

KOLBE, R. W. - 1932 - Grundlinien einer allgemeinen Ökologie der Diatomeen; *Ergebn. Biol.* 8: *221—348*.

KOLKWITZ, R. and MARSSON, M. - 1908 - Ökologie der pflanzlichen Saprobien; *Ber. dtsch. bot. Ges.* 26a: *505—519*.

LINDEMAN, R. L. - 1942 - The trophic-dynamic aspect of ecology. *Ecology* 23: *399—418*.

LIST, H. - 1930 - Die Entwicklungsgeschichte von *Cladophora glomerata* Kützing; *Arch. Protistenk.* 72: *453—481*.

NORTON, J. F. (Ed.) - 1946 - Standard methods for the examination of water and sewage. xvii, 286 pp. New York.

PIA, J. - 1933 - Kohlensäure und Kalk. Einführung in das Verständnis ihres Verhaltens in den Binnengewässern. *In:* A. THIENEMANN, *Die Binnengewässer*, Bd. 13. 183 pp.

PURDY, W. C. - 1916 - Potomac plankton and environmental factors. *In:* H. S. CUMMING, Investigation of pollution and sanitary conditions of the Potomac watershed with special reference to self purification and the sanitary condition of shellfish in the lower Potomac River; *(U.S.A.) Hygienic Lab. Bull. Publ. Health Serv.* 104, pp. *130—191*.

—— 1922 - A study of the pollution and natural purification of the Ohio River; *(U.S.A.) Publ. Health Bull.* 131: i—v, *1—78*.

—— 1930 - A study of the pollution and natural purification of the Illinois River. II. The plankton and related organisms; *(U.S.A.) Publ. Health Bull.* 198. xvi, 212 pp.

RAABE, HILDEGARD - 1951 - Die Diatomeenflora der ostholsteinischen Fliessgewässer; *Arch. Hydrobiol.* 44: *521—638*.

REINHARD, E. G. - 1931 - The plankton ecology of the upper Mississippi, Minneapolis to Winona; *Ecol. Monogr.* 1: *395—464*.

ROACH, L. S. - 1932 - An ecological study of the plankton of the Hocking River; *Bull. Ohio Biol. Survey* 5: *253—279*.

RUSSELL, I. C. and LEVERETT, F. - 1908 - Description of the Ann Arbor Quad-
    rangle. *In:* Geologic Atlas of the United States, Fol. 155, 15 pp., 4 pl.
    Washington.

SCHRÖDER, H. - 1939 - Die Algenflora der Mulde: Ein Beitrag zur Biologie
    Saprober Flüsse. *In:* R. KOLKWITZ, *Pflanzenforschung* 21. vi, 88 pp.

THURMAN, MARTHA H. and KUEHNE, R. A. - 1952 - An ecological study of
    Cladophora glomerata (Chlorophyceae) near Dallas; *Field & Lab.* 20:
    26—28.

USPENSKI, E. E. - 1927 - Eisen als Faktor für die Verbreitung niederer Wasser-
    pflanzen. *In:* R. KOLKWITZ, *Pflanzenforschung* 9. vi, 104 pp.

VERDUIN, J. - 1951 - A comparison of phytoplankton data obtained by a
    mobile sampling method with those obtained from a single station;
    Amer. J. Bot. 38: *5—11.*

WASER, E. BLÖCHLIGER, G. and THOMAS, E. A. - 1943 - Untersuchungen am
    Rhein von Schaffhausen bis Kaiserstuhl 1938—1939 und 1940—1941;
    Z. Hydrol. 9: *225—309.*

WELCH, P. S. - 1948 - Limnological methods. xviii, 381 pp. Philadelphia.
——— 1952. Limnology. xi, 538 pp. New York.

WHITFORD, L. A. - 1956 - The communities of algae in the springs and spring
    streams of Florida; *Ecology* 37: *433—442.*

Author's address: Canisius College,
Buffalo, N.Y., U.S.A.

Fig. 1. Map of the Saline River, with outlines showing the limits of its basin. Heavy numbers refer to stations mentioned in this study. Numbers preceded by a „T" refer to the tributaries. — Fig. 2. Schematic surface view of the *Spirogyra* community just below Station 15. Water enters from the left (Riffle 15) and is deflected by the far bank, forming two principal eddies. Differences in rate of flow are suggested by length of arrows on the map. A, shoal area; B, backwater area. Background shading indicates *Spirogira* community on shallow bottom. Intensely shaded small areas indicate *Spirogyra* masses which have risen to surface; some of these from Shoal A are being carried downstream. — Fig. 3. Diagram of a vertical section through the crustose *Phormidium-Schizothrix* community. Faint vertical lines, as at d, indicate orientation of *Schizothrix* filaments; heavier vertical lines, as at a, indicate filaments of *Audouinella violacea*; b, *Cladophora glomerata*; c, encrusted filaments of *Cladophora glomerata*; e, galleries in the algal crust constructed by Trichoptera larvae.
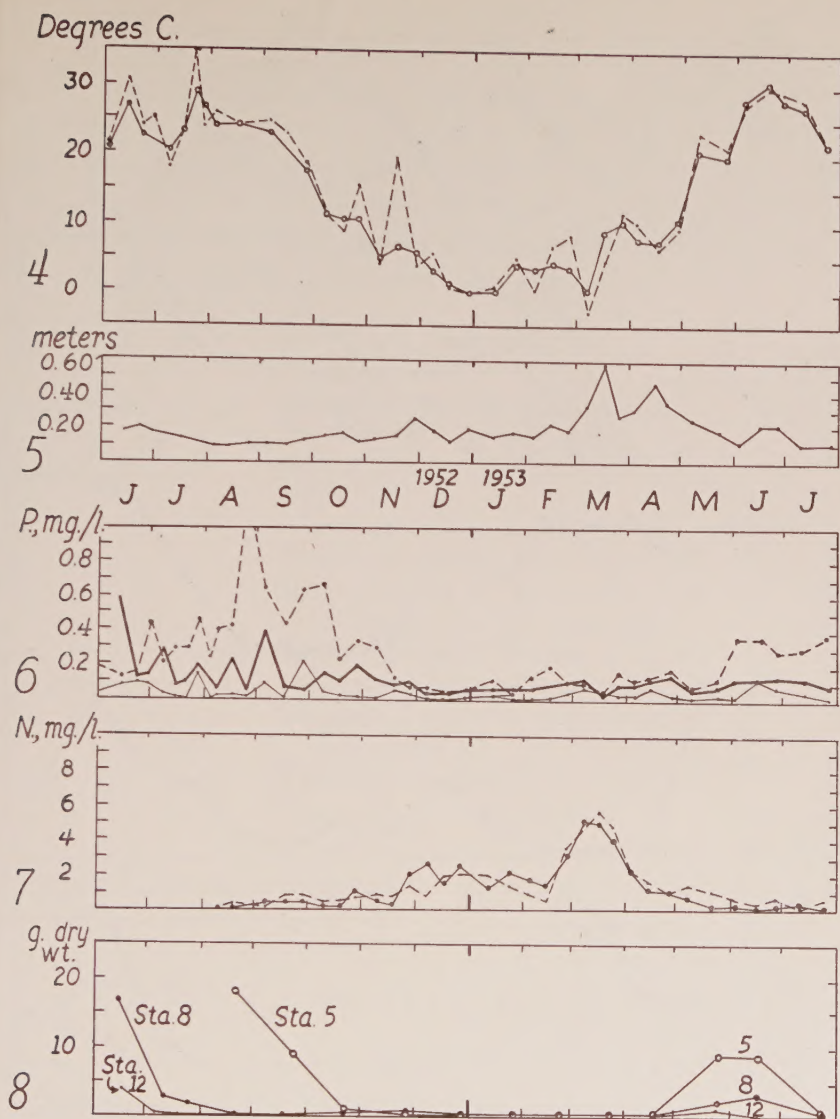
Fig. 4. Temperature of air (broken line) and of Saline River water (solid line) on sampling days from June 3, 1952, to July 25, 1953. — Fig. 5. Water level at Station 8. — Fig. 6. Seasonal variation in inorganic phosphate phosphorus in selected portions of the Saline River during the period June 1952 to July 1953; faint solid line, average of headwater Stations 5, 8, and 12; heavy solid line, average of β-mesosaprobic Stations 25 and 28; broken line, average of polysaprobic Stations 15 and 18. — Fig. 7. Seasonal variation in nitrate nitrogen in selected portions of the Saline River; solid line, average of headwater Stations 5, 8, and 12; broken line, average of polysaprobic Stations 15 and 18. — Fig. 8. Seasonal variation in dry weight of *Cladophora glomerata* removed from ten arbitrarily selected rocks as described in text; numbers refer to the three headwater stations (5, 8 and 12) at which this sampling was done.

407

KEY:

——————— *Diatoma vulgare* •••••••••• *Gomphonema olivac.*

——————— *Cladophora glom.* — — — — — *Nitzschia palea*

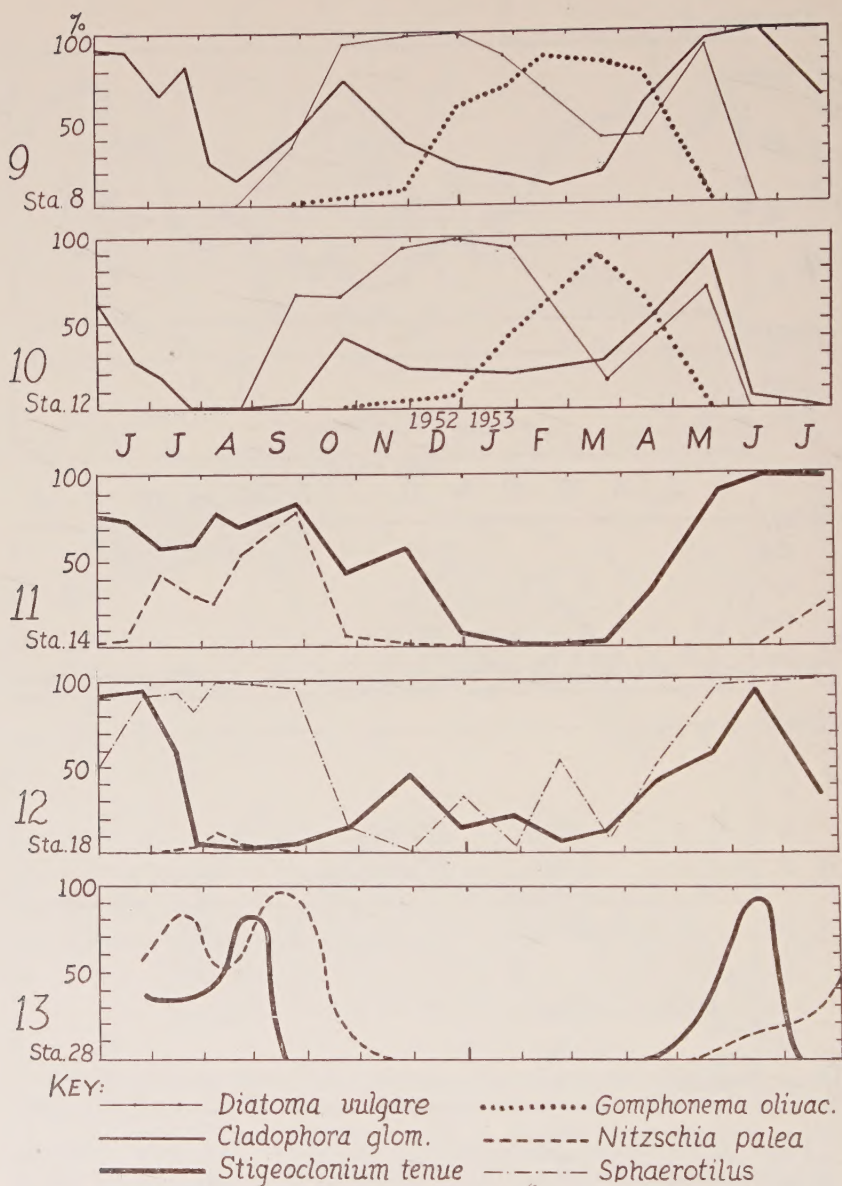▬▬▬▬▬ *Stigeoclonium tenue* — ·— ·— ·— *Sphaerotilus*

Fig. 9. Seasonal variation in frequency of important algae at Station 8 (unpolluted). — Fig. 10. Seasonal variation in frequency of important algae at Station 12 (unpolluted, heavily shaded in summer). — Fig. 11. Seasonal variation in frequency of important algae at Station 14 (effects of industrial pollution). — Fig. 12. Seasonal variation in frequency of algae at Station 18 (effects of industrial pollution plus sewage). — Fig. 13. Seasonal variation in estimated frequency of *Stigeoclonium tenue* and *Nitzschia palea* at Station 28, showing recovery after pollution (β-mesosaprobic); the curves in Figure 13 are not based on measured transects, but on visual estimates.

UITGEVERIJ DR. W. JUNK, DEN HAAG

PUBLISHERS-VERLAG-EDITEURS

Biologia et Industria
Biologisch Jaarboek
Coleopterorum Catalogus
Documenta Ophthalmologica
Enzymologia, acta biocatalytica
Flora Neerlandica
Fossilium Catalogus I (Animalia)
Fossilium Catalogus II (Plantae)
Hydrobiologia, acta hydrobiologica,
    hydrografica et protistologica
Monographiae Biologicae
Mycopathologia et Mycologia Applicata
Qualitas Plantarum et Materiae
    Vegetabiles
Tabulae Biologicae
Vegetatio, acta geobotanica

TABULAE BIOLOGICAE

Editors:

G. BACKMAN, *Lund* - A. FODOR, *Jerusalem* - A. FREY-WYSSLING, *Zürich*
A. C. IVY, *Chicago* - V. J. KONINGSBERGER, *Utrecht* - A. S. PARKES, *London*
A. C. REDFIELD, *Woods Hole, Mass.* - E. J. SLIJPER, *Amsterdam*
H. J. VONK, *Utrecht*

Scope: Constants and Data (with some didactic context) from all parts of
biology and border-line sciences, selected and established by competent
specialists. Quotations of all the original works for further reference. Text
in English, French, German. Headings in the index also in Italian and in Latin.

SPECIAL VOLUMES:

Vol. XIX: CELLULA (4 parts) complete. 1939—1951 . . . .   f 148.—
Vol. XXI: DIGESTIO (4 parts) complete. 1946—1954 . . . .   f 290.—
              part 3/4 Evertebrates (with index) 1954 . . . . · f 140.—

Vol. IX   Nr. 4

CONTENTS